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TAXONOMIC REVISIONS OF SOME UPPER CAMBRIAN AND LOWER ORDOVICIAN CONODONTS WITH COMMENTS ON THEIR EVOLUTION[1]

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ABSTRACT

The generic classification of Upper Cambrian and lowermost Ordovician conodonts has been revised in accord with multielement taxonomic concepts. Several species are reassigned from form taxonomy to new genera based on multielement apparatuses. New genera include *Albiconus, Eoconodontus, Monocostodus, Nogamiconus, Teridontus,* and *Utahconus. Muellerodus,* n. gen., is proposed to replace *Muellerina* Szaniawski, 1971, which is a junior homonym of *Muellerina* Bassiouni, 1965, an ostracode. Taxonomy of *Cordylodus* Pander and various species assigned to it is extensively emended, and the genus is interpreted to possess a two-element apparatus. *Semiacontiodus* Miller is emended to include two-element apparatuses. *Proconodontus* Miller is emended and interpreted as having a one-element apparatus. New species described are *Albiconus postcostatus, Cordylodus drucei, Proconodontus posterocostatus, P. tenuiserratus,* and *Utahconus tenuis.* The holotype of *Nericodus capillamentum* Lindström is figured and interpreted as being broken. Lectotypes are designated for *Fryxellodontus inornatus* and *F. lineatus,* the genus being restricted to these two species.

Two distinct lineages of euconodonts can be recognized in upper Franconian strata. A *Proconodontus* lineage diversified in the Trempealeauan and developed several related two-element apparatuses (e.g., *Eoconodontus, Cambrooistodus, Cordylodus). Cambrooistodus* did not survive into the Ordovician, a time when *Cordylodus* underwent much diversification. A *Teridontus* lineage was endemic to Australasia during the Late Cambrian and evolved little. Following the latest Cambrian extinction within the *Proconodontus* lineage, the *Teridontus* lineage rapidly produced additional genera with a variety of one-element apparatuses (e.g., *Hirsutodontus, Clavohamulus, Monocostodus)* and two-element apparatuses (e.g., *Semiacontiodus, Utahconus).* General evolutionary trends include differentiation of the posterior edge of elements (development of keels, costae, and adenticulate and denticulate processes), shortening of basal cavities, development of white matter, and thickening of walls with reduction of basal cones.

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INTRODUCTION

During preparation of descriptions of Cambrian and lowermost Ordovician conodont genera for the revision of Part W of the *Treatise on Invertebrate Paleontology*, it became clear that considerable taxonomic revision of these genera was needed. It is the purpose of this paper to clarify the generic classification of a number of Upper Cambrian and Lower Ordovician conodonts. Most of the changes involve description of new genera with previously named type species, the changes being necessary because of recognition that these species belong to previously unrecognized conodont apparatuses.

Of the new genera, three are paraconodonts. *Albiconus* has a previously undescribed type species. It is the last known paraconodont genus to appear and is probably represented by a one-element apparatus. *Nogamiconus* is established for several species of probable one-element apparatuses. *Muellerodus* is proposed to replace *Muellerina* Szaniawski, 1971, which is preoccupied by *Muellerina* Bassiouni, 1965, an ostracode.

Several primitive euconodont genera considered here are also based on one-element apparatuses. One such genus, *Proconodontus* Miller, 1969, is redefined and two new species, *P. posterocostatus* and *P. tenuiserratus*, are described. *Clavohamulus* Furnish, 1938, *Hirsutodontus* Miller, 1969, and *Teridontus*, n. gen., also include one-element apparatuses.

Simple cones of the new euconodont genus *Monocostodus* form a primitive symmetry transition by variation in the lateral and posterior position of a single costa.

Several genera are based on two-element apparatuses. These include the related new genera *Cambrooistodus* and *Eoconodontus*, which possess similar noncostate apparatuses, and differ from *Semiacontiodus* Miller, 1969, and *Utahconus*, n. gen., which possess similar costate apparatuses. *Cordylodus* Pander, 1856, is extensively revised and is interpreted to include a two-element denticulate apparatus similar to those of *Cambrooistodus* and *Eoconodontus*.

The apparatus of *Fryxellodontus* Miller, 1969, was originally interpreted as a three- or four-element symmetry-transition series. Designation of holotypes for the two species described by Miller (1969) was improper and lectotypes are designated here.

Examination by electron microscopy of the holotype of *Nericodus capillamentum* Lindström, 1955, has shown it to be a broken element. The obscure species, which is known only from this specimen and a few additional fragments, may be related to *Hirsutodontus*.

The geographic and stratigraphic occurrences for most species are referenced where appropriate; unreferenced occurrences are from my research collections. Biostratigraphic ranges of taxa are listed for most North American occurrences, and are given (Fig. 1) in terms of either trilobite zones (Winston & Nicholls, 1967; Longacre, 1970; Stitt, 1977) or conodont zones and faunal units (Miller, 1975, 1978; Ethington & Clark, 1971).

Illustrated specimens have been placed in the collections of the National Museum of Natural History, Washington, D.C., and are identified by numbers with the prefix "USNM."

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TERMINOLOGY OF DISCRETE ELEMENTS

In discussing multielement conodont taxa it is necessary to refer to the discrete elements. Recently, several systems for naming such elements have been introduced, but none has been universally accepted. The apparatuses discussed here are relatively simple, and complex terminology is unnecessary. Accordingly, individual elements are described using adjectives that refer to distinctive morphologic characters. Examples include **unicostate** and **bicostate** elements of *Utahconus*, n. gen., and **symmetrical** and **asymmetrical** elements of *Semiacontiodus* Miller.

A special set of terms for elements of *Fryxellodontus* Miller was introduced when I

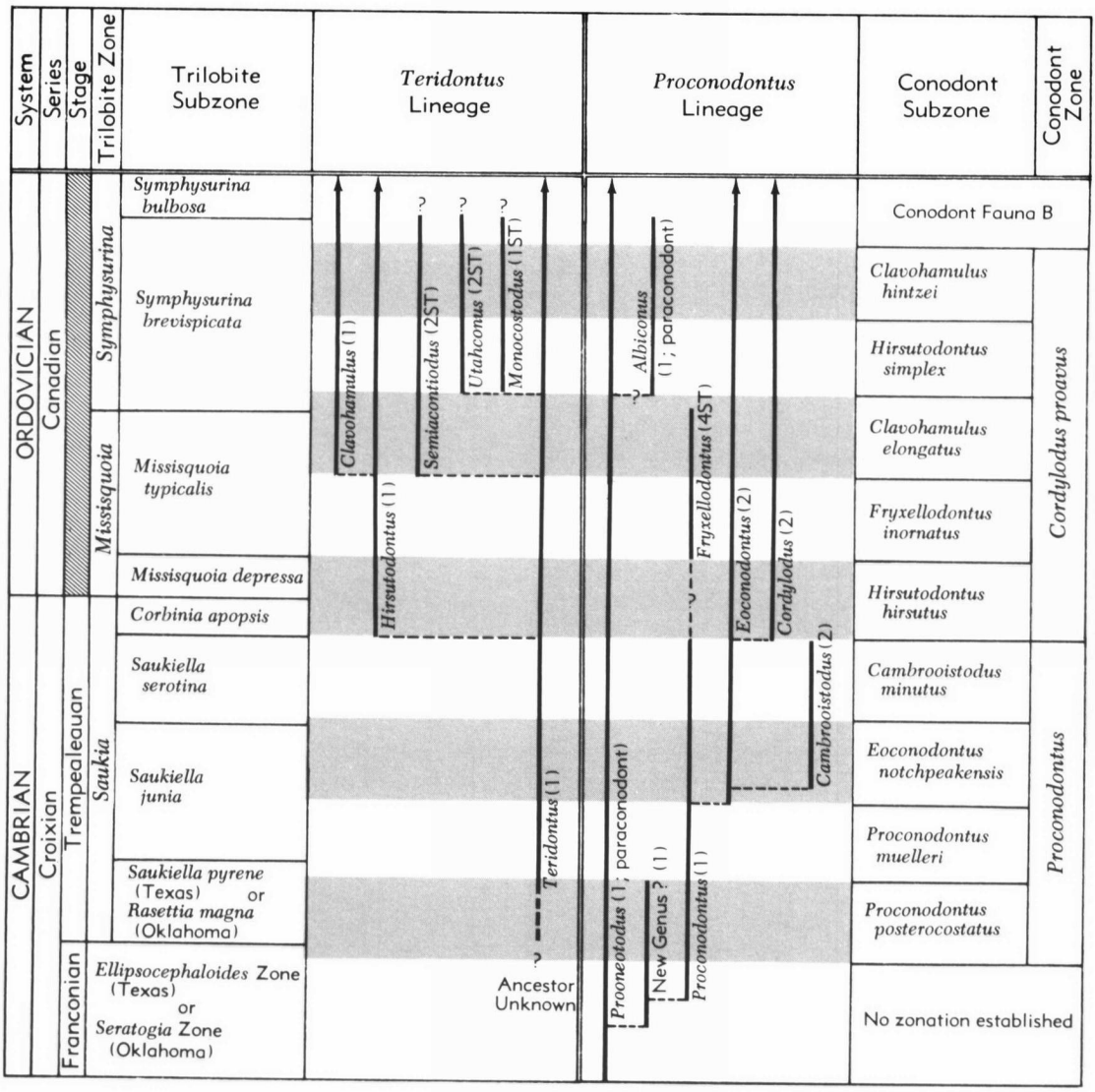

Fig. 1. Inferred phylogeny of some Upper Cambrian and Lower Ordovician conodont genera. Number and letter codes indicate type of apparatus for each genus: 1, one-element apparatus; 2, two-element apparatus; 1ST, one-element apparatus with symmetry transition; 2ST, two-element apparatus with symmetry transition; 4ST, four-element apparatus with symmetry transition. Conodont biostratigraphy is after Miller (1975, 1978) and trilobite biostratigraphy is after Winston and Nicholls (1967) and Longacre (1970) for Texas and Stitt (1977) for Oklahoma.

named the genus. These terms, planus, serratus, intermedius, and symmetricus, are replaced here by **planar, serrate, intermediate,** and **symmetrical,** respectively.

A uniform set of terms is used for the homologous elements of *Cambrooistodus,* n. gen., *Cordylodus* Pander, and *Eoconodontus,* n. gen. Each genus consists of two elements, referred to here as **rounded** and **compressed.** Rounded elements are round to oval in cross section, commonly have smooth anterior and posterior edges, and are bilaterally symmetrical or nearly so. Compressed elements are oval in cross section, have sharp anterior and posterior edges, and are usually strongly asymmetrical owing to lateral bending of the cusp and a carina on the inner edge of the basal margin.

EVOLUTIONARY RELATIONSHIPS

Evolutionary relationships among early euconodont genera are now rather well understood and have been useful in generic classification. These relationships are diagrammatically shown on Figure 1, where the apparatus for each genus is coded so that evolution of the various types can be more easily comprehended. Upper Cambrian and lowermost Ordovician euconodonts can be divided into two evolutionary lineages, one including *Proconodontus* and the other *Teridontus.* Both lineages appear in the upper Franconian and seem to have separate ancestry, which would make the euconodonts polyphyletic.

The Proconodontus *lineage.*—Based on stratigraphic position and morphology, *Proconodontus* appears to be one of the most primitive conodontophorid genera. An apparent transition from the paraconodont *Prooneotodus* Müller and Nogami to a probable new euconodont genus to primitive species of *Proconodontus* Miller is known from the Wilberns Formation of Texas (see discussion under *Proconodontus tenuiserratus,* n. sp.). Histological investigations in progress may clarify this transition between the two orders. Species of *Proconodontus* have thin walls surrounding prominent basal cones, they have basal cavities extending to the tips, and they lack white matter. Interspecific evolution involved development and elaboration of anterior and posterior keels (discussed under each species). Elements of *Proconodontus* species are common in North American Trempealeauan conodont faunas.

In middle Trempealeauan strata (lower *Saukiella junia* Subzone, Fig. 1), a single euconodont species, *Proconodontus muelleri* Miller, ranges through a considerable interval. This species is abruptly joined near the middle of the *S. junia* Subzone by two conodont form-species, originally described as *Proconodontus notchpeakensis* and *P. carinatus* (Miller, 1969). These differ from *P. muelleri,* from which they clearly evolved, in possessing shorter basal cavities and cusps composed of white matter. *"P." notchpeakensis* is a nearly symmetrical form, whereas *"P." carinatus* is strongly bent laterally and has a lateral carina. These two forms invariably first occur at the same horizon in many stratigraphic sections, and they are nearly always found together throughout the upper Trempealeauan and well into the Ordovician *Symphysurina* Zone. I consider them to represent a single apparatus with two elements, which is sufficiently different from its one-element ancestor to require a separate generic name. Here described as *Eoconodontus,* n. gen., the two form-species are synonymized under the name *Eoconodontus notchpeakensis* (Miller). The original *"P. notchpeakensis"* is the rounded element and *"P. carinatus"* is the compressed element. *E. notchpeakensis* may have been the first conodont apparatus with more than one element (Fig. 1), and it was the first conodont in the *Proconodontus* lineage with white matter.

In strata slightly above the first occurrence of *Eoconodontus notchpeakensis* is found another form-species, described as *Oistodus cambricus* (Miller, 1969). This compressed element was clearly derived from the compressed element of *E. notchpeakensis* but differs in having an adenticulate posterior process that joins the posterior edge of the cusp at a sharp and usually acute angle. Because there is no new corresponding rounded element, I conclude that the newly evolved compressed element was part of a new apparatus in which the rounded element was identical (or nearly identical) to the rounded element of its ancestor, *E. notchpeakensis.*

The type species of *Cambrooistodus*, n. gen., is based on this new apparatus. *Cambrooistodus cambricus* (Miller) and its smaller descendant, *C. minutus* (Miller), are characteristic but not abundant in North American upper Trempealeauan conodont faunas.

The boundary between the *Proconodontus* and the *Cordylodus proavus* zones is important in conodont evolution because several genera terminate or begin their ranges at this horizon (Fig. 1). Species that disappear at the top of the *Proconodontus* Zone include *Proconodontus muelleri, P. serratus, Cambrooistodus cambricus,* and *C. minutus.* These disappearances correspond with those of many trilobite species. The only euconodont species found in both zones is *Eoconodontus notchpeakensis;* however, several long-ranging paraconodont species are found in both zones. *Cordylodus proavus, Teridontus nakamurai, Hirsutodontus hirsutus,* and *H. rarus* first appear at the base of the *C. proavus* Zone.

Cordylodus proavus is interpreted here as a two-element apparatus consisting of rounded (form-species *C. proavus* Müller) and compressed (form-species *C. oklahomensis* Müller) elements. Clearly, these were derived from the rounded and compressed elements, respectively, of *Eoconodontus notchpeakensis,* from which they differ principally in the presence of secondary denticles (Pl. 1). *C. proavus* is the ancestor of several other species of *Cordylodus,* whereas other direct descendants of *E. notchpeakensis* have not been identified.

Fryxellodontus may be a part of the *Proconodontus* lineage, but the relationship is uncertain. This unusual conodont apparatus consists of four elements that form a symmetry transition. The basal cavities are deep and some elements have a prominent posterior keel, features present in *Proconodontus muelleri.* In samples with abundant *Fryxellodontus inornatus,* a few elements show similarity to *P. muelleri;* however, it is possible that these specimens are unusual or pathologic variants. The ancestry of *Fryxellodontus* remains uncertain, and it may represent an unrelated lineage.

Several general patterns of evolution can be identified in the *Proconodontus* lineage. First, the posterior edge of the cusp became differentiated in a variety of ways. The most primitive species, *Proconodontus tenuiserratus,* n. sp., had a faintly serrated keel that became more prominent and nonserrate in *P. posterocostatus,* n. sp. In *P. muelleri* an anterior keel was added, and finally on *P. serratus* the posterior keel again became serrate. On *Cambrooistodus* an adenticulate posterior process developed on the compressed element. The denticles of *Cordylodus* are another modification of the posterior edge of the base.

A second evolutionary trend was progressive shortening of the basal cavities of all genera. The basal cavities of *Proconodontus* extend to the tips of elements, but in *Eoconodontus* they are shorter. Among the oldest Cambrian elements of *E. notchpeakensis* the basal cavities are much deeper than in Ordovician elements. The same trend is seen in *Cambrooistodus,* in which *C. minutus* has shallower basal cavities than its ancestor, *C. cambricus.* In the evolution of *Cordylodus,* younger species have shorter basal cavities than older species, and the shapes of basal cavities also change. The anterior edges of the basal cavities of *C. proavus* curve convexly, in *C. intermedius* and *C. drucei,* n. sp., they curve concavely, and in *C. angulatus* and *C. rotundatus* they are recurved sigmoidally. *Cordylodus lindstromi* has extensions of the basal cavities into one or more denticles.

A third evolutionary trend is the development of white matter. *Proconodontus* elements lack white matter, but it solidly fills the cusps of *Eoconodontus* elements, beginning just above the tips of the basal cavities. As basal cavity depth decreased in *Eoconodontus, Cambrooistodus,* and *Cordylodus,* the amount of white matter increased. Additional wisps of white matter developed outside of the basal cavity below its tip. In *Cordylodus* elements the secondary denticles are mostly composed of white matter. In the upper part of Fauna B some specimens, which may represent *Drepanodus* and may be derived from *Eoconodontus,* show early stages of development of a growth axis. In these specimens only the center of the cusp is white matter, and a thin layer of clear apatite surrounds it. The taxonomy of these elements is problematical and beyond the scope of this paper.

A fourth evolutionary trend in the *Proconodontus* lineage involves changes in thick-

ness of the wall and the basal cone. The most primitive species of *Proconodontus* have prominent basal cones and thin, easily exfoliated walls. In *P. muelleri* the walls are much thicker, but the basal cone is still prominent. As the basal cavities and basal cones became shorter in *Eoconodontus* and its descendants, the walls of the elements became progressively more prominent than the basal cones. In Ordovician representatives of the *Proconodontus* lineage, the basal cones are still present but are not so prominent as in Cambrian forms.

Proconodontus, Eoconodontus, Cambrooistodus, and *Cordylodus* are a related evolutionary complex among early euconodonts. Although *Cordylodus* has a cosmopolitan distribution in the Ordovician, distribution of the Upper Cambrian genera is not as widespread. The entire sequence of *Proconodontus* species is known only in the United States and Australia, although *P. muelleri* and *P. serratus* are known from Iran. *Eoconodontus* is known from North America, Australia, and is widespread in Asia. *Cambrooistodus* is known only from North America.

The most interesting feature of the distribution of the *Proconodontus* lineage is its absence from the Upper Cambrian of northern Europe. Müller (1959) studied numerous samples from throughout the Upper Cambrian of Sweden and reported a diverse paraconodont fauna extending virtually to the top of the Cambrian; euconodont elements of the *Proconodontus* lineage are apparently lacking. In North America many of Müller's paraconodont species are reported from Franconian strata, but in uppermost Franconian and Trempealeauan strata the paraconodont fauna partly disappeared as the *Proconodontus* lineage appeared and diversified. Many of the uppermost Cambrian paraconodont species that Müller described from northern Europe are unknown in North America. The reasons for this important difference in distribution pattern are uncertain, but the contrasts in depositional environments and paleogeography between North America and northern Europe are probably important factors.

The Teridontus *lineage.*—Whereas the *Proconodontus* lineage diversified during both the Late Cambrian and Early Ordovician, the *Teridontus* lineage mostly diversified during the Ordovician. The oldest representative of the *Teridontus* lineage is *T. nakamurai* (Nogami), which in most of North America does not occur below the base of the *Cordylodus proavus* Zone (Fig. 1). The species is abundant above this horizon, and is a distinctive element of the *C. proavus* Zone and Ordovician Fauna B above. In China and Australia, however, *T. nakamurai* is recorded far below the top of the Upper Cambrian. I have seen specimens from the Chatsworth Limestone at the Black Mountain section of Druce and Jones (1971) that are tentatively assigned to this species; however, the distribution of white matter is rather different from that in elements occurring in the *C. proavus* Zone of the United States. Further study may result in assignment to a different species, but these Australian specimens are closely related to *T. nakamurai.*

Twenty elements from the upper Franconian and lower Trempealeauan strata of central Texas have been provisionally identified as *Teridontus nakamurai.* The oldest of these were associated with the youngest known specimens of *Proconodontus tenuiserratus,* n. sp., which represent an early stage of one transition from paraconodont to euconodont structure. The coeval specimens of *T. nakamurai* apparently represent an unrelated lineage of euconodonts whose unknown ancestors may have existed earlier in Asia and Australia.

Although the *Proconodontus* lineage evolved rapidly during Late Cambrian time, the *Teridontus* lineage evolved little. Druce and Jones (1971) reported elements of *T. nakamurai* throughout much of the Upper Cambrian strata that they studied in Australia, but they documented no descendants of this species within the interval. Coeval strata in North America generally lack *Teridontus* elements, but recently I have found such elements at two horizons in shallow cratonal deposits in Texas. These occurrences may represent migrations of *Teridontus* from the Australasian area. The sparseness of faunas recovered in Texas may indicate that the emigrants were unsuccessful competitors with endemic species of the *Proconodontus* lineage.

Diversification of the *Teridontus* lineage is recorded in uppermost Cambrian and Lower

Ordovician strata. Following the extinction of species of the *Proconodontus* lineage during latest Cambrian time, elements of the *Teridontus* lineage abruptly appeared in North American shallow marine deposits. These faunas may represent opportunistic migrants that, because of little competition, quickly adapted to available food and habitats. At the base of the *Cordylodus proavus* Zone, *Teridontus nakamurai* and an apparent descendant, *Hirsutodontus hirsutus*, are found in many parts of North America, and elements of *T. nakamurai* and *H. hirsutus* are fairly common in basal Ordovician shallow marine deposits. Before *C. proavus* produced its first descendant, *C. intermedius*, the *Teridontus* lineage generated many forms: *Hirsutodontus hirsutus* gave rise to *H. rarus*, which in turn produced several species of *Clavohamulus*, and *H. hirsutus* also produced the large-spined *H. simplex*. *T. nakamurai* produced the costate simple-cone genera *Monocostodus*, *Semiacontiodus*, and *Utahconus*, each with a different apparatus. The ranges of these taxa, based on earlier nomenclature (Miller, 1969), have recently been published (Miller, 1978, table 2), and evolutionary relationships are indicated on Figure 1.

Some general evolutionary trends of the *Teridontus* lineage are similar to those of the *Proconodontus* lineage. First, posterior and lateral faces on elements of the *Teridontus* lineage became differentiated. Whereas keels and denticles developed in the *Proconodontus* lineage, single or multiple costae developed on genera (*Monocostodus*, *Semiacontiodus*) of the *Teridontus* lineage. Keeled asymmetrical carinate cusps with a lateral carina and posterior adenticulate process developed in both *Cambrooistodus* and *Utahconus*; however, spinose and granulose sculpture in the *Teridontus* lineage (*Hirsutodontus*, *Clavohamulus*) has no parallel in the *Proconodontus* lineage.

The ratios of symmetrical to asymmetrical elements in some apparatuses differ in the two lineages. In the *Proconodontus* lineage, *Eoconodontus* (n. gen.) and *Cordylodus* (as emended) have symmetrical (rounded) elements that are much more abundant than asymmetrical (compressed) elements. In the *Teridontus* lineage, *Semiacontiodus* (as emended) has symmetrical (bicostate) elements that are much less abundant than asymmetrical (unicostate) elements. These differences suggest that the respective elements may have occupied different positions or performed different functions in the animal.

Other evolutionary trends of the *Proconodontus* lineage: shortening of the basal cavity, development of white matter, and thickening of the basal wall, are unknown in the *Teridontus* lineage. The oldest known specimens of *Teridontus* have short basal cavities with the tip of the cusp composed partly of white matter, and although a basal cone is present, the wall of the base is relatively thick. Presumably the lineage had a paraconodont ancestor, and paraconodonts generally have deep basal cavities, lack white matter, and have thin walls. The stage of histological development of *Teridontus* is comparable to *Eoconodontus* in the *Proconodontus* lineage. A more primitive stage of the *Teridontus* lineage can be postulated in which the basal cavity was much deeper, the cusp lacked white matter, and a thin basal wall covered a prominent basal cone. This postulated transition between paraconodont and *Teridontus* histology is comparable to *Proconodontus* in its lineage. Knowledge of the Cambrian history of the *Teridontus* lineage is limited, but this postulated ancestor may have lived during Dresbachian or early Franconian time in the Australasian area.

Genera of the *Teridontus* lineage have variable distribution in conodont faunas of earliest Ordovician age. All genera are widely distributed in North America. In Australia, all genera except *Clavohamulus* have been described by Druce and Jones (1971), and they also described several species that probably belong to this lineage but are unknown elsewhere (e.g., *"Oneotodus" bicuspatus*). *Teridontus* has been widely reported in Asia (Iran, Korea, China, Siberia), but other genera are not so widespread. Outside of North America and Australia, *Hirsutodontus*, *Clavohamulus*, and *Semiacontiodus* have been reported in Siberia, and *Utahconus* is known from Turkey.

Although not considered in detail, I believe that many of the simple-cone genera of

the middle and upper Lower Ordovician are related to the *Teridontus* lineage. These younger genera are widespread, but they have disjunct, provincial distributions. Probably more genera of the Lower Ordovician faunas are related to the *Teridontus* lineage than to the *Proconodontus* lineage. Possibly other genera are unrelated to either of these lineages.

Morphologic convergence is a problem in studying the evolution of post-*Cordylodus proavus* conodont faunas. Specimens provisionally assigned to *Drepanodus (sensu lato)* may be evolutionary offshoots from *Eoconodontus*, *Teridontus*, and *Monocostodus*. Microsculpture may prove to be useful in separating elements of the *Proconodontus* and *Teridontus* lineages in the Lower Ordovician. Well-preserved specimens of *Teridontus* and some of its descendants (e.g., *Monocostodus* and *Semiacontiodus)* are covered by fine striae (Pl. 2, fig. 16), whereas *Eoconodontus* and its descendants lack this microsculpture (Pl. 1, fig. 12). The original collections of *Drepanodus subarcuatus* Furnish, 1938, including the syntypes, consist of specimens that are striated *(Teridontus* lineage) and specimens that are smooth *(Proconodontus* lineage). These examples illustrate the magnitude of the problem, and considerable additional work is needed.

SYSTEMATIC DESCRIPTIONS

Genus ALBICONUS, new

Type species.—*Albiconus postcostatus*, n. sp.

Description.—One-element apparatus of symmetrical simple cones, proclined to erect; base narrow, tapering gently to tip, tip bent posteriorly; basal cavity extending to tip; anterior face flat, posterior margin drawn out into prominent costa; cross section roundly triangular.

Discussion.—*Albiconus*, a probable paraconodont, is the youngest genus to appear in the paraconodont lineage; however, species of other paraconodont genera extend into strata higher than the highest occurrence of *Albiconus*.

Tentative assignment of *Albiconus* to the paraconodonts is made on the basis of its white color. Paraconodont elements from northern Europe are commonly black due to preservation of an outer organic layer; however, such a layer is apparently not preserved on paraconodont elements from western North America, and the apatite is white or rarely clear. Associated euconodonts are amber or gray.

Albiconus is monotypic, but three species described from the Tremadocian of Sweden by Van Wamel (1974), *Coelocerodontus bicostatus*, *C. latus*, and *C. variabilis*, are possibly congeneric.

ALBICONUS POSTCOSTATUS, new species

Figure 2

Holotype.—USNM 303279 (Figure 2A-C).

Description.—Because the genus is monotypic, the species definition is the same as that for the genus.

Discussion.—Although several hundred elements of *A. postcostatus* are white, the color may differ in areas where oxidation has not removed the outer organic layer. Many elements, including the holotype, show the greatest width somewhat above the base, and the width tapers slightly toward the base. On many other elements the greatest width is at the base.

The ancestor of *A. postcostatus* is not known surely, but the species is similar to *Prooneotodus rotundatus* (Druce & Jones) and may be derived from it.

Occurrence.—*Albiconus postcostatus* is known from Utah (lower House Limestone, House Range; listed as "new genus of paraconodont" by Miller, 1978, table 2), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), and Alberta, Canada (Putty Shale Member of Survey Peak Formation; Derby, Lane, & Norford, 1972). Associated trilobites in these areas are from the *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone. The species occurs in the

Fig. 2. *Albiconus postcostatus*, n. gen. and n. sp.——A-C. Posterior, posterobasal, and lateral views of holotype from base of House Limestone, Lower Ordovician, Sevier Lake section of Miller (1969), southern House Range, Utah; X60, 100, 60; USNM 303279.——D. Lateral view and line drawings showing basal cavity (D') and transverse section (D") of paratype from 9 m (28 ft) above base of House Limestone, Lower Ordovician, north side of Sneakover Pass, central House Range, Utah; X60, USNM 303280.

Hirsutodontus simplex and *Clavohamulus hintzei* subzones of the *Cordylodus proavus* Zone and in lower Fauna B.

Genus CAMBROOISTODUS, new

Type species.—*Oistodus cambricus* Miller, 1969, p. 431.

Description.—Two-element apparatus composed of erect to reclined simple cone elements. Characteristic compressed element robust to moderate in size, asymmetrical due to lateral bending of cusp; basal cavity very deep in primitive forms to shallow in more advanced forms, cusp correspondingly short to long, varying inversely with depth of basal cavity; cusp composed of white matter, strongly compressed laterally, with prominent anterior and posterior keels; inner side of base with prominent bulge (carina); upper edge of posterior adenticulate process meeting posterior keel at sharp, usually acute, angle. Less distinctive rounded element symmetrical, proclined to reclined, oval to round in cross section; anterior and posterior edges may be sharp or rounded; basal cavity very deep to shallow and cusp correspondingly short to long and composed of white matter; posterior edge of base forming smooth concave curve. Evidence of microsculpture lacking on faces of both elements, even at high magnification.

Discussion.—Two species are referred to this genus. They were originally described as *Oistodus cambricus* Miller, 1969, and *O. minutus* Miller, 1969; however, Lindström (1973) correctly pointed out that these species should no longer be referred to *Oistodus* Pander, and he referred them to *Proconodontus* Miller. He also discussed possible synonymies among *"Proconodontus" notchpeakensis*, *"P." carinatus*, *"P." cambricus*, and *"P." minutus*. A better understanding of this group of species has become possible only after detailed sampling in many Upper Cambrian sections where details of the evolution of these species have been determined. The first two of the four species are here considered to be elements of *Eoconodontus notchpeakensis*, and the latter two are referred to *Cambrooistodus*. *E. notchpeakensis* is the ancestor of *C. cambricus*, which is the ancestor of *C. minutus*, and all have similar apparatuses. The rounded elements of all three species are presently indistinguishable from one another, and in samples containing more than one of these species, only the compressed elements can be identified. The compressed element of *Eoconodontus* lacks the posterior process of *Cambrooistodus*.

Cambrooistodus differs from *Oistodus* Pander by possessing a cusp composed of white matter rather than hyaline material. *Drepanoistodus* Lindström and *Paroistodus* Lindström are Lower Ordovician genera that may have been derived from *Cambrooistodus*. The relationship is uncertain because a considerable stratigraphic gap separates the uppermost occurrence of *Cambrooistodus* (top of *Proconodontus* Zone) from the lowermost occurrence of *Drepanoistodus* and *Paroistodus* (upper Tremadocian). All three genera have similar apparatuses, but the details of shape, particularly of the basal cavity, are very different.

CAMBROOISTODUS CAMBRICUS (Miller)

Figure 3A, 4E; Plate 1, figure 9

Oistodus cambricus Miller, 1969, p. 431, text-

fig. 5A, pl. 66, figs. 8-12.

Proconodontus cambricus Lindström, 1973, p. 399, 400, 402, 403.

?*Oistodus* cf. *O. cambricus* Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, fig. 19.

Proconodontus carinatus Miller (part), 1969, p. 437, pl. 66, figs. 13, 14 (*not* figs. 15-20).

Discussion.—Some compressed elements previously assigned to *Proconodontus carinatus* (Miller, 1969, pl. 66, figs. 13, 14) are here reassigned to *C. cambricus*. In these rare elements the edge of the posterior process meets the posterior keel at a sharp but obtuse angle, whereas the angle is acute in most compressed elements.

Cambrooistodus cambricus differs from its apparent descendant, *C. minutus* (Miller), in being more robust and in having a deeper basal cavity.

Occurrence.—*C. cambricus* is known only in North America, from Utah (middle and upper members of Notch Peak Formation; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range), Oklahoma (Signal Mountain Limestone, Wichita Mountains), Texas (San Saba Member of Wilberns Formation, Llano uplift), and Alberta, Canada (basal silty member of Survey Peak Formation; Derby, Lane, & Norford, 1972). Associated trilobites in these strata represent the upper part of the *Saukiella junia* Subzone

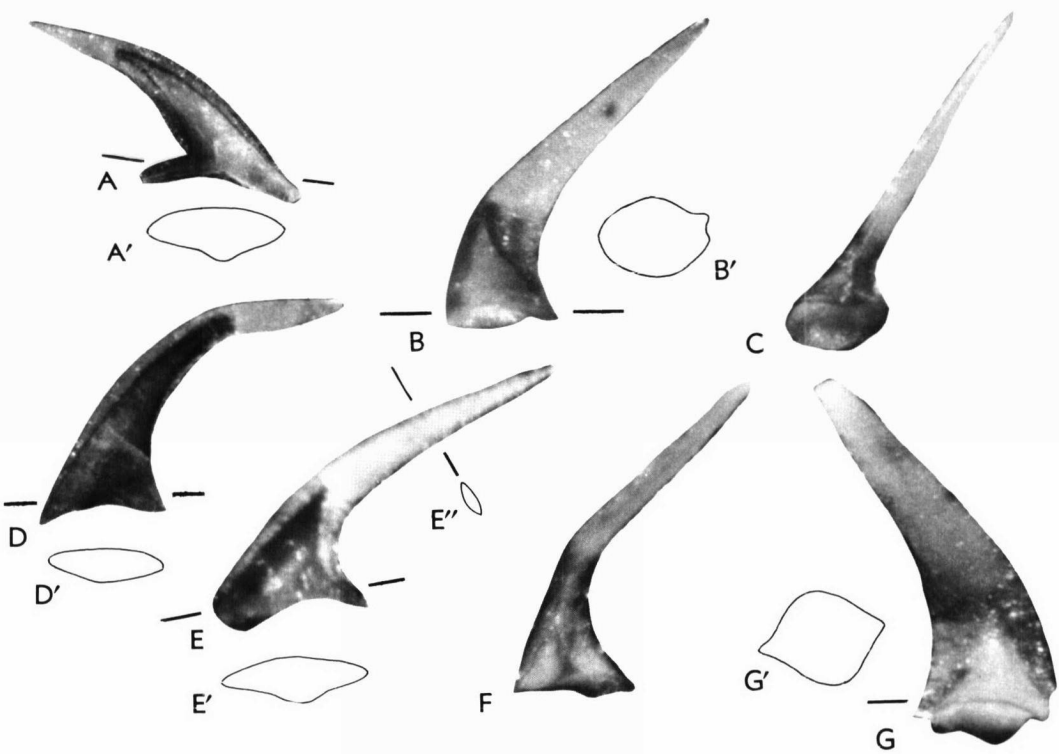

Fig. 3. Elements of three genera, illustrating shape of basal cavity and distribution of white matter——A. *Cambrooistodus cambricus* (Miller); lateral view and transverse section of compressed element from San Saba Member of Wilberns Formation, Llano uplift, Texas; 415 m (1,360 ft) above base of Threadgill Creek section of Barnes and Bell (1977), X55, USNM 303420.——B,C,F,G. *Utahconus utahensis* (Miller) from Signal Mountain Limestone, Wichita Mountains, Oklahoma, 530 m (1,735 ft) above base of measured section of Stitt (1977); lateral view (B) with transverse section (B′), and posterior view (C) of unicostate element, X110, USNM 303431; lateral (F) and posterior views (G) with transverse section (G′) of bicostate element, X110, USNM 303430.——D,E. *Eoconodontus notchpeakensis* (Miller) from same formation and horizon as A; lateral views with transverse sections of rounded element (D,D′) USNM 303416, and compressed element (E,E′), USNM 303417; both X110.

and the *Saukiella serotina* Subzone of the *Saukia* Zone. The species occurs in the *Eoconodontus notchpeakensis* and *Cambrooistodus minutus* subzones of the *Proconodontus* Zone.

The specimen reported by Tipnis, Chatterton, and Ludvigsen (1978) from the District of Mackenzie, Canada, cannot be assigned with certainty to this species because of the poor quality of illustration. The associated fauna seems to indicate an earliest Ordovician age.

CAMBROOISTODUS MINUTUS (Miller)

Figure 4F; Plate 1, figure 8

Oistodus minutus Miller (part), 1969, p. 433, text-fig. 5B, pl. 66, figs. 1-4 (*not* figs. 5-7); *not* Özgül and Gedik, 1973, p. 48, pl. 1, figs. 21, 22.

Discussion.—Two Lower Ordovician elements formerly assigned to *Oistodus minutus*, one from Utah (Miller, 1969, pl. 66, figs. 5-7) and one from Turkey (Özgül & Gedik, 1973, pl. 1, figs. 21, 22), here are assigned to *Utahconus tenuis*, n. gen. and n. sp. This reassignment considerably shortens the observed stratigraphic range of the revised *C. minutus*, which is now known only from the Upper Cambrian.

Occurrence.—The geographic distribution of revised *C. minutus* is similar to that of *C. cambricus*, except that the former is not present in the District of Mackenzie, Canada. *C. minutus* is known only from the *Saukiella serotina* Subzone of the *Saukia* Zone and the *Cambrooistodus minutus* Subzone of the *Proconodontus* Zone.

Genus CLAVOHAMULUS Furnish, 1938

Type species.—*Clavohamulus densus* Furnish, 1938, by original designation.

Discussion.—Furnish (1938) described only one species of the genus, and no new species were described until 1969 when several more primitive species and an emended concept of the genus were published (Miller, 1969). Lindström (1973) further discussed the genus and recognized all of the described species, although he suggested that *Clavohamulus primitus* Miller might be a junior synonym of *C. elongatus* Miller. The two species have very similar morphology and virtually identical stratigraphic ranges, and accordingly Lindström's suggested synonymy is accepted here. Lindström (1973, p. 55) also discussed the affinity of *Clavohamulus* Furnish to *Hirsutodontus* Miller and (p. 117) reassigned *Oneotodus bulbousus* Miller, 1969, to *Hirsutodontus*. Because of its granulose ornamentation (Miller & Kurtz, 1975), however, the species now is assigned to *Clavohamulus*. Thus, *Clavohamulus* includes at least five species: *Clavohamulus densus* Furnish, 1938; *C. bulbousus* (Miller), 1969; *C. elongatus* Miller, 1969; *C. hintzei* Miller, 1969; and *C. triangularis* Abaimova, 1975.

Clavohamulus seems to have possessed a simple, one-element apparatus.

Genus CORDYLODUS Pander, 1856

Type species.—*Cordylodus angulatus* Pander, 1856, p. 33, subsequent designation by Ulrich and Bassler, 1926, p. 8.

Emended description.—Two-element apparatus; both elements simple and usually possessing posterior denticulate process, although denticle(s) may arise directly from posterior edge of cusp in primitive specimens. Rounded element usually symmetrical, with rounded cusp and denticles; denticles separated from one another at bases. Except in advanced species, compressed element asymmetrical due to lateral bending of cusp and denticles, and because of prominent bulge (carina) on inner side of process; cusp and denticles strongly compressed laterally and possessing sharp edges; denticles fused at bases. Rounded element usually at least twice as abundant as compressed element.

Discussion.—*Cordylodus* elements are an important and nearly ubiquitous component of uppermost Cambrian and lowermost Ordovician conodont faunas. Study of thousands of elements of the several described form-species resulted in several conclusions: 1) *Cordylodus* evolved from *Eoconodontus*, n. gen.; 2) like its ancestor, *Cordylodus* is a two-element assemblage; 3) the basal cavities of *Cordylodus* elements are of critical importance in understanding the morphology, taxonomy, and evolution of the genus; 4)

Cordylodus mostly is confined to the uppermost Cambrian and part of the Lower Ordovician (Faunas A to C of Ethington & Clark, 1971); some younger species previously referred to *Cordylodus* should be reassigned to other genera; and 5) the suggestion of various authors that *C. angulatus* Pander and *C. rotundatus* Pander form a single apparatus is probably incorrect.

Miller (1969) showed that the form-species *C. proavus* Müller, 1959, evolved from *Proconodontus notchpeakensis* Miller, 1969, and that the form-species *C. oklahomensis* Müller, 1959, evolved from *P. carinatus* Miller, 1969. Further study has reinforced this conclusion, although these two form-species of *Proconodontus* are here interpreted to be the rounded and compressed elements, respectively, of a single multielement species referred to as *Eoconodontus notchpeakensis* (Miller). The morphology of *C. proavus* and *C. oklahomensis* is similar to that of *Eoconodontus*, except for the presence of denticles.

The two form-species of *Cordylodus* first appear at the same stratigraphic horizon (base of *Corbinia apopsis* Subzone, uppermost Cambrian) in many measured sections. They are virtually always found together and the *C. proavus* element is nearly always at least twice as abundant as the *C. oklahomensis* element. Therefore, it is concluded that elements of these two form-taxa constitute a single two-element species, *Cordylodus proavus* Müller. This revised species is abundant through the upper 40 m of the Notch Peak Formation and lower 30 m of the House Limestone of western Utah and through about 90 m of the upper Signal Mountain Limestone in the Wichita Mountains, Oklahoma. In these areas (and in thinner time-equivalent strata in many other areas), *C. proavus* is the only species of *Cordylodus* found in the interval, which includes the *Corbinia apopsis* Subzone of the *Saukia* Zone, and the *Missisquoia* and lower *Symphysurina* zones. This interval includes most of Fauna A of Ethington and Clark (1971).

In Utah, Oklahoma, and in several other areas of the western United States, younger strata (upper Fauna A and Fauna B of Ethington & Clark) contain less abundant elements of *C. proavus*, but several additional elements of *Cordylodus* species are abundant. Only some of these elements have been described. Rounded elements include the form-species *C. intermedius* Furnish (*sensu* Druce & Jones, 1971), *"C. insertus"* MS Miller, 1970 *(nomen nudum)*, and an undescribed form-species incorrectly identified as *C. rotundatus* by Miller (1970). Compressed elements include *C. lindstromi* Druce and Jones, 1971, an undescribed form-species incorrectly identified as *C. prion* by Miller (1970), and in some sections the form-species *C. prion* Lindström, 1955. These form-species all first occur either in the upper part of Fauna A, which has been called the *Cordylodus proavus* Zone by Miller (1978), or in Fauna B, and they seem to have evolved from elements of *C. proavus*. Can they be joined together into logical two-element species, using *C. proavus* as a model?

The first descendant of *C. proavus* appears in the upper part of the *Cordylodus proavus* Zone. This is *C. intermedius* Furnish, which is characterized by a basal cavity with concavely curved anterior edges. Near the base of Fauna B another descendant appears with a similar type of basal cavity. This is *C. drucei*, n. sp., which differs from *C. intermedius* by possessing a basal carina on the rounded element. Somewhat above the base of Fauna B each species gave rise to a species in which the anterior edges of the basal cavities are strongly curved concavely and the tips are recurved sigmoidally. The descendant of *C. intermedius* is *C. angulatus*, and the descendant of *C. drucei* is *C. rotundatus*. These species are mostly distinguished by their rounded elements.

At the base of Fauna B, *Cordylodus proavus* produced another offspring, *C. lindstromi*, in which both elements have extensions of the basal cavity into the first denticle. Descendants of this species are unknown.

Species of *Cordylodus* are biostratigraphically useful in Lower Ordovician strata in many parts of the world. In North America they are common in Lower Ordovician faunas A to C of Ethington and Clark (1971), but they are usually absent in younger strata.

Specimens of *"Cordylodus" horridus* and *"C." ramosus* illustrated by Barnes and Poplawski (1973) appear to be plausable Middle Ordovician descendants of rounded and compressed elements, respectively, of *C. rotundatus*; however, Barnes and Poplawski stated that *"C." ramosus* consists of a transition

series, and that associated strata contain cordylodiform, ligonodiniform, hibbardelliform, and cladognathodiform elements of this transition series. Therefore, they emended the concept of *Cordylodus* to include such complex transition series. Because elements of such forms are not associated with the apparatus of the type species of *Cordylodus*, I reject that emendation and assign to *Cordylodus* (emended herein) only species with apparatuses that consist of simple, rounded and compressed, denticulate elements. Species with additional elements or different elements should be assigned to other genera. Accordingly, *"Cordylodus" horridus* Barnes and Poplawski, 1973, and *"Cordylodus" ramosus* Hadding, 1913 (*sensu* Barnes & Poplawski, 1973), are excluded from *Cordylodus* and should be reassigned to an appropriate genus by future workers.

Some authors have assigned compressed elements of *Cordylodus* to *Cyrtoniodus* Stauffer, 1935; however, *Cyrtoniodus* is of Middle Ordovician age and not closely related to *Cordylodus*. *Subcordylodus* Stauffer, 1935, is likewise regarded as being unrelated to *Cordylodus*.

CORDYLODUS ANGULATUS Pander

Figure 4Q, R?; Plate 1, figure 22, 23?

Cordylodus angulatus Pander, 1856, p. 33, pl. 2, figs. 27-31, pl. 3, fig. 10; Lindström (part), 1955, p. 551, text-fig. 3G (*not* text-fig. 3E), pl. 5, fig. 9(?); ?Ethington and Clark, 1965, p. 189, pl. 1, fig. 7; Druce and Jones (part), 1971, p. 66, text-fig. 23a, b, pl. 3, figs. 4-6 (*not* fig. 7); Jones, 1971, p. 45, pl. 8, figs. 3a-c; Ethington and Clark (part), 1971, pl. 1, figs. 16, 20 (*not* fig. 15); Müller, 1973, p. 27, text-fig. 2G, 3, pl. 11, figs. 1-5, ?6, 7; *not* Van Wamel, 1974, p. 58, pl. 1, figs. 5-7; Viira (part), 1974, p. 63, text-fig. 4c (*not* text-figs. 4a, b), pl. 1, figs. 1-3, 11-13 (*not* fig. 8); *not* Repetski and Ethington, 1977, pl. 1, fig. 3.

Cordylodus sp. A Druce and Jones, 1971, p. 72, text-fig. 23U, pl. 10, fig. 10.

(In part) *Cordylodus prion* Lindström, 1955, p. 552, pl. 5, figs. 14-16; Druce and Jones, 1971, p. 70, text-fig. 23i, k-o, pl. 2, figs. 1-7; Müller, 1973, p. 33, text-fig. 2E, 8, pl. 10, fig. 4; *not* Van Wamel, 1974, p. 59, pl. 1, figs. 8-9; ?Viira (part), 1974, p. 63, pl. 1, fig. 7 (*not* fig. 6).

(In part) *Cyrtoniodus prion* Ethington and Clark, 1971, pl. 1, fig. 21; Miller, 1971, p. 79, pl. 1, figs. 14-16 (*not* fig. 17).

Emended description.—Rounded element with cusp and denticles rounded in cross section and composed mostly of white matter. Basal cavity commonly shallow but may be moderately deep, usually extending not higher than top of posterior denticulate process; anterior edge of basal cavity strongly concave and tip recurved sigmoidally, usually with sharp horizontal U-curve near mid-height of basal cavity; anterobasal margin usually somewhat rounded; lateral faces of posterior process straight and smooth, without bulges on either side.

Compressed element usually symmetrical or nearly so, with long posterior denticulate process; cusp and denticles compressed laterally and possessing sharp edges; denticles fused at bases. Cusp may be bent slightly to one side; in primitive elements, slight bulge (carina) may exist on concave (inner) side near basal margin. Basal cavity moderately deep to shallow, usually extending to near top of posterior process. Anterior edge of basal cavity usually convexly curved but may be concavely curved in some elements. Compressed elements less abundant than rounded elements, and may be absent in upper part of species range.

Discussion.—Several rounded elements assigned to *C. angulatus* by previous authors are reassigned to other species as follows: Lindström (1955, text-fig. 3E), reassigned to *C. lindstromi;* Druce and Jones (1971, pl. 3, fig. 7), reassigned to *C. drucei*, n. sp.; Ethington and Clark (1971, pl. 1, fig. 15) and Repetski and Ethington (1977, pl. 1, fig. 3), both judged to be an undescribed species of *Cordylodus;* Van Wamel (1974, pl. 1, fig. 5-7), of which figure 5 is reassigned to *C. proavus* and figures 6 and 7 are reassigned to *C. intermedius;* and Viira (1974, text-fig. 4a, b, pl. 1, fig. 8), reassigned to *C. intermedius*. Several compressed elements are likewise reassigned, including specimens figured by Van Wamel (1974, pl. 1, figs. 8, 9) and Viira (1974,

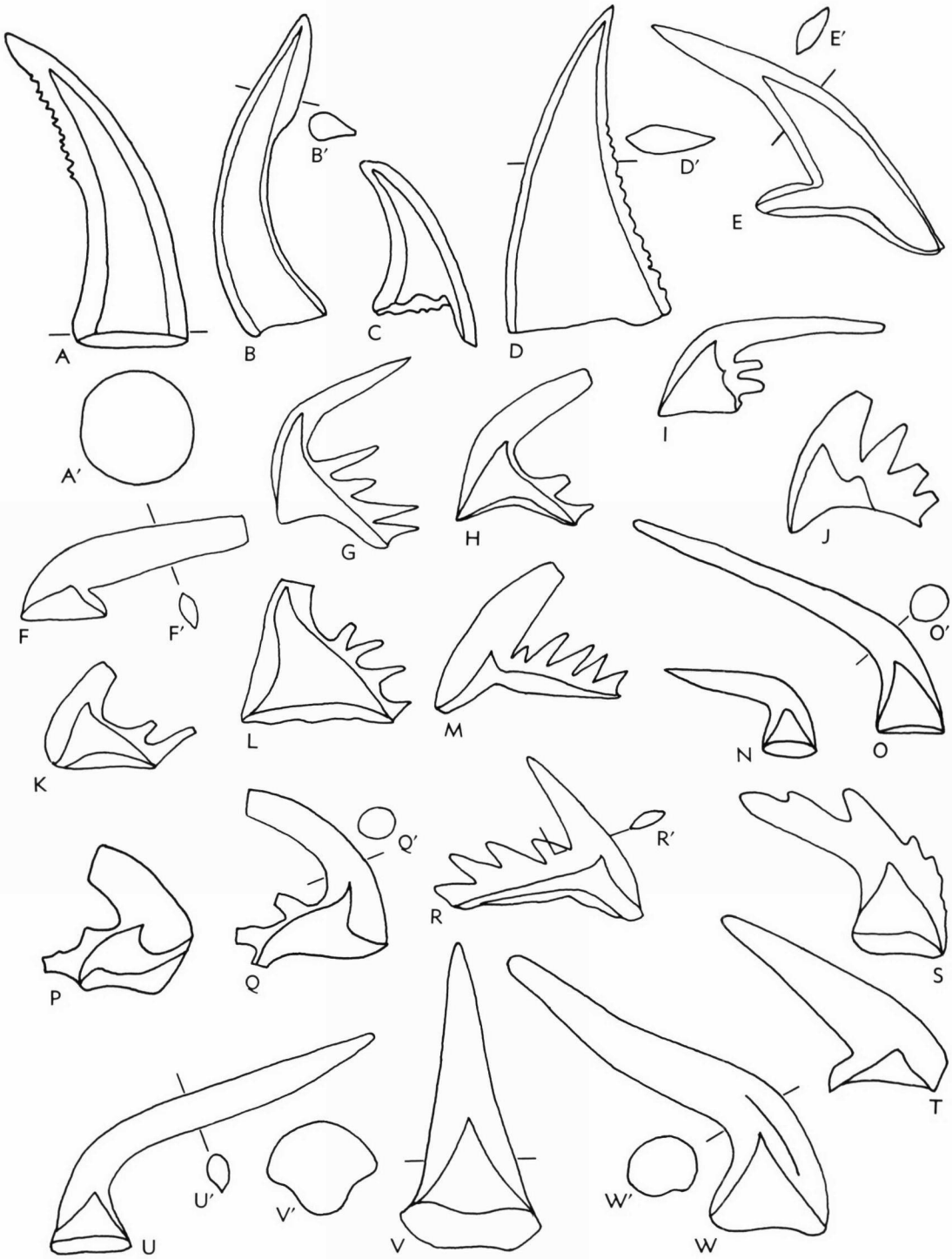

Fig. 4. Outlines of various conodont elements showing shapes of basal cavities and, for some, transverse sections (prime letters)——A. *Proconodontus tenuiserratus*, n. sp. (holotype, Pl. 1, fig. 2).——B. *Proconodontus posterocostatus*, n.

pl. 1, fig. 6), both reassigned to *C. intermedius;* and one by Miller (1971, pl. 1, fig. 17), reassigned to *C. lindstromi.* Shape of the basal cavity is the main criterion on which these reassignments are made.

Cordylodus angulatus apparently evolved from *C. intermedius,* from which it differs principally in the shape of the basal cavity of the rounded element. Pander (1856, pl. 3, fig. 10) illustrated a rounded element that I judge to be a primitive representative of *C. angulatus;* however, the tip of the basal cavity is recurved slightly. Druce and Jones (1971, text-fig. 23C) have illustrated a rounded element of *Cordylodus* that has a basal cavity similar to that in Pander's figure except that the tip is not recurved. Therefore, it is referred to *C. intermedius* and is interpreted as an advanced representative of that species. These are examples of transitional rounded elements near the point where the two species are separated. A more typical rounded element of *C. angulatus* was illustrated by Müller (1973, text-fig. 23G). The rounded element of *C. angulatus* is necessary to permit recognition of this species because the compressed elements of several species of *Cordylodus* are similar.

The compressed elements of *C. angulatus* have been described as the form species *Cordylodus prion* Lindström. This is the only compressed element found by Lindström (1955) associated with *C. angulatus* in the Baltic region, which is the type area for both form-species. These two elements are also associated in other areas where *C. angulatus* is found. The form-species *C. prion* is also found associated with rounded elements of *C. rotundatus, C. intermedius,* and *C. drucei,* n. sp. Therefore, "*C. prion*" probably was a part of the apparatus of all three species. The compressed elements of species of *Cordylodus* seemingly evolved more slowly than the rounded elements and are less distinctive.

Compressed elements of all species of *Cordylodus* are less commonly found than rounded elements, and compressed elements seem to have become relatively less abundant through time. In the upper part of the range of *C. angulatus,* compressed elements may be lacking entirely. This is interpreted to mark the culmination of a progressive evolutionary trend. Thus, in advanced representatives, *C. angulatus* may have possessed a one-element apparatus. The same trend is observed in advanced *C. rotundatus,* and it is judged unnecessary to create a new genus or species for such apparatuses.

The common association of the form-species *C. angulatus* and *C. rotundatus* has caused several authors to conclude that these formed a single apparatus. This conclusion is rejected here because such an apparatus is so unlike those of earlier species of *Cordylodus.* All older species of *Cordylodus* have apparatuses consisting of both rounded elements and compressed elements, whereas the form-species *C. angulatus* and *C. rotundatus* are both rounded elements. These two elements also have different ancestors: *C. intermedius* is the ancestor of *C. angulatus,* whereas *C. drucei* is the ancestor of *C. rotundatus.* Also, *C. rotundatus* has a strongly rounded antero-basal margin and a bulge (carina) on one side of the posterior process, whereas both of these features are lacking on *C. angulatus.*

Occurrence.—*C. angulatus* is widely distributed and in North America is known from Utah (House Limestone, House Range; Eth-

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Fig. 4. Continued from facing page.

sp. (holotype, Pl. 1, fig. 4).——C. *Proconodontus muelleri* Miller (Pl. 1, fig. 7).——D. *Proconodontus serratus* Miller (Pl.1, fig. 13).——E. *Cambrooistodus cambricus* (Miller) (Pl.1, fig. 9).——F. *Cambrooistodus minutus* (Miller) (Pl. 1, fig. 8).——G,H. *Cordylodus proavus* Müller, rounded (G) element (Pl. 1, fig. 14) and compressed (H) element (Pl. 1, fig. 15).——I,J. *Cordylodus lindstromi* Druce and Jones, rounded (I) element (Pl. 1, fig. 18) and compressed (J) element (Pl. 1, fig. 19).——K. *Cordylodus drucei,* n. sp., rounded element (holotype; Pl. 1, figs. 20, 21).——L. *Cordylodus intermedius* Furnish, rounded element (Pl. 1, fig. 16)——M. *Cordylodus intermedius?* Furnish or *C. drucei?,* n. sp., compressed element (Pl. 1, fig. 17).——N. *Hirsutodontus hirsutus* Miller (Pl. 2, fig. 14).——O. *Teridontus nakamurai* (Nogami) (Pl. 2, figs. 15, 16).——P. *Cordylodus rotundatus* Pander, rounded element (Pl. 1, fig. 24).——Q. *Cordylodus angulatus* Pander, rounded element (Pl. 1, fig. 22).——R. *Cordylodus angulatus?* Pander or *C. rotundatus?* Pander, compressed element (Pl. 1, fig. 23).——S. *Hirsutodontus simplex* (Druce & Jones).——T. *Utahconus tenuis,* n. sp., bicostate element (holotype, Pl. 2, fig. 6).——U. *Monocostodus sevierensis* (Miller) (Pl. 2, figs. 8, 9).——V,W. *Semiacontiodus nogamii* Miller, symmetrical (V) element (Pl. 2, figs. 10, 11) and asymmetrical (W) element (Pl. 2, fig. 12). Figures not drawn to same scale.

ington & Clark, 1971; Garden City Limestone, Wasatch Range; Mason, 1975), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (uppermost San Saba Member of Wilberns Formation and lower Threadgill Member of Tanyard Formation, Llano uplift), Pennsylvania-Maryland (upper Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), and Wyoming-Montana (Lower Ordovician of Bighorn Mountains; Kurtz, 1978). Elsewhere, *C. angulatus* is known from northwestern Greenland (Stouge, 1977), Scandinavia (Lindström, 1955; Van Wamel, 1974), Soviet Union (Viira, 1974), Australia (Druce & Jones, 1971; Jones, 1971), and Iran (Müller, 1973). In North America the species is found in Fauna B (except lowermost part) and lower Fauna C of Ethington and Clark (1971). Lindström (1955, pl. 9) recorded *C. angulatus* through the upper Tremadocian and into the lower Arenigian of Scandinavia.

CORDYLODUS DRUCEI, new species

Figure 4K, M; Plate 1, figures 17?, 20, 21, 25

Cordylodus angulatus Druce and Jones (part), 1971, p. 66, pl. 3, fig. 7 (*not* figs. 4-6).

Cordylodus cf. *C. intermedius* Abaimova (part), 1975, text-fig. 8.42 (*not* 8.34), pl. 10, fig. 10.

(In part) *Cordylodus oklahomensis* Druce and Jones, 1971, p. 69, text-fig. 23j, pl. 5, figs. 6, 7; ?Jones, 1971, p. 47, pl. 2, figs. 5-8.

(In part) *Cordylodus prion* Druce and Jones, 1971, p. 70, text-figs. 23i, k-o, pl. 2, figs. 1-7; *not* Lindström, 1955, p. 552, pl. 2, figs. 14-16; *not* Müller, 1973, p. 33, text-fig. 2E, 8, pl. 10, fig. 4; *not* Van Wamel, 1974, p. 59, pl. 1, figs. 8-9; *not* Viira, 1974, p. 63, pl. 1, figs. 6, 7.

not Cyrtoniodus prion Ethington and Clark, 1971, pl. 1, fig. 21; Miller, 1971, p. 79, pl. 1, figs. 14-17.

Holotype.—Rounded element, USNM 303283 (Fig. 4k; Pl. 1, figs. 20, 21).

Description.—Relatively rare species with distinctive rounded element and somewhat variable compressed element. Rounded element asymmetrical with bulge (carina) on one side of base beneath anterior end of denticulate process; axis of bulge trending posteriorly and downward. Cusp and denticles with rounded edges; denticles separated at bases. Basal cavity relatively shallow with apex extending slightly above top of posterior process, anterior edge concave or straight, apex not recurved. Anterobasal corner a sharp angle in primitive elements, but somewhat rounded in more advanced elements.

Compressed elements less distinctive, may include two forms. More distinctive form asymmetrical due to lateral bending and to presence of bulge (carina) on inner side of base. Distinctive basal cavity curving concavely on anterior edge, then bending sharply near anterobasal corner and subparallel to basal margin. Basal cavity moderately deep, apex usually at least as high as top of posterior process but may be shallower in advanced elements. Second form symmetrical or nearly so; cusp may be bent slightly to one side and slight bulge (carina) may exist on inner side near basal margin. Anterior edge of basal cavity usually convexly curved and extending about to top of posterior process. Both types of compressed elements have laterally compressed cusps and denticles with sharp edges; denticles fused at bases.

Discussion.—Two rounded elements, one illustrated by Druce and Jones (1971, pl. 3, fig. 7) as *C. angulatus* and one illustrated by Abaimova (1975, text-fig. 8.42, pl. 10, fig. 10) as *C. intermedius*, have the distinctive characteristics of the rounded element of *C. drucei*, and they are here reassigned to this new species.

The rounded element of *C. drucei* is necessary to permit recognition of this species because of the variability of the compressed elements and their similarity to those of other coeval species of *Cordylodus*. The asymmetrical form is similar to the compressed element of *C. intermedius*, and the symmetrical form is similar to the compressed elements of *C. angulatus* and *C. rotundatus*. The conclusion that both types of compressed elements were associated with the distinctive rounded element of *C. drucei* is uncertain and is based on the occurrence together of all three elements in many samples.

Cordylodus drucei has three distinguishing characteristics: a concave anterior edge of the

basal cavity, a sharp anterobasal corner, and a carina on one side of the posterior process. *C. proavus* differs in having a convex anterior edge of the basal cavity and in lacking a carina. In *C. rotundatus* the anterior edge of the basal cavity is more convex and the tip is recurved, the anterobasal margin is well rounded, and the basal margin is usually arched. *C. intermedius* and *C. angulatus* differ in lacking a carina on the posterior process.

Occurrence.—In the United States *C. drucei* is known from Utah (lower House Limestone, House Range), Nevada (lower House Limestone, southern Egan Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), and Texas (upper San Saba Member of Wilberns Formation and lowermost Threadgill Member of Tanyard Formation, Llano uplift); all elements represent uppermost *Cordylodus proavus* Zone or Fauna B. Elsewhere the species is known from Canada (Putty Shale Member of Survey Peak Formation, Alberta), Australia (Druce & Jones, 1971), and the eastern Soviet Union (Abaimova, 1975).

Etymology.—Named in honor of Edric Druce, Bureau of Mineral Resources, Australia, for his important work on Cambrian and Ordovician conodonts.

CORDYLODUS INTERMEDIUS Furnish

Figure 4L, M?; Plate 1, figures 16, 17?

Cordylodus intermedius Furnish, 1938, p. 338, text-fig. 2C, pl. 42, fig. 31; Druce and Jones, 1971, p. 68, text-figs. 23f, g, pl. 3, figs. 1-3; Jones, 1971, p. 46, pl. 2, figs. 2, 3; Abaimova, 1972, text-fig. 1; Müller, 1973, p. 30, text-figs. 2C, 4, pl. 10, figs. 1-3.

?*Cordylodus* cf. *C. intermedius* Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, fig. 7.

not Cordylodus cf. *C. intermedius* Abaimova, 1975, text-fig. ?8.34, 8.42, pl. 10, fig. 10.

Cordylodus cf. *C. angulatus* Druce and Jones, 1971, p. 67, text-fig. 23c.

Cordylodus angulatus Van Wamel, 1974, p. 58, pl. 1, figs. 6, 7; Viira (part), 1974, p. 63, text-fig. 4a, b, (*not* 4c), pl. 1, fig. 8 (*not* figs. 1-3, 11-13).

Cordylodus caseyi Druce and Jones, 1971, p. 67, text-figs. 23d, e, pl. 2, figs. 9-12; Jones, 1971, p. 46, pl. 2, fig. 1; Abaimova, 1975, p. 109, text-fig. 8.41, pl. 10, fig. 3.

Cordylodus lenzi Müller, 1973, p. 31, text-figs. 2F, 5, pl. 10, figs. 5-9.

(In part) *Cordylodus oklahomensis* Druce and Jones, 1971, p. 69, text-fig. 23j, pl. 5, figs. 6, 7; ?Jones, 1971, p. 47, pl. 2, figs. 5-8.

(In part) *Cordylodus prion* Druce and Jones, 1971, p. 70, text-figs. 23i, k-o, pl. 2, figs. 1-7.

Cordylodus prion Müller, 1973, p. 33, text-figs. 2E, 8, pl. 10, fig. 4; Van Wamel, 1974, p. 59, pl. 1, figs. 8-9; ?Viira (part), 1974, p. 63, pl. 1, fig. 6 (*not* fig. 7); *not* Lindström, 1955, p. 552, pl. 5, figs. 14-16.

(In part) *Cyrtoniodus prion* Ethington & Clark, 1971, pl. 1, fig. 21; Miller, 1971, p. 79, pl. 1, figs. 14-16 (*not* fig. 17).

Cordylodus proavus Druce and Jones (part), 1971, p. 70, text-fig. 23p, pl. 1, fig. 1 (*not* figs. 2-6).

Emended description.—Rounded element, distinctive basal cavity with anterior edge concave or straight. Compressed elements variable; cusp and denticles laterally compressed and with sharp edges, denticles fused at bases; elements may be symmetrical or asymmetrical due to slight lateral bending of cusp and presence of slight bulge (carina) on inner side of basal margin; anterior edge of basal cavity convex, or concave with sharp bend so that anterobasal part of cavity subparallel to basal margin of element; apex of basal cavity ending slightly above or below top of posterior process.

Discussion.—As recognized by Druce and Jones (1971), *Cordylodus intermedius* is the evolutionary intermediate between *C. proavus* and *C. angulatus*. This is indicated best by the shape of the basal cavities in the rounded elements and also in some of the compressed elements. Forms identified as *C. oklahomensis* by Druce and Jones (1971) and as *Cyrtoniodus prion* by Miller (1970) have a concave anterior edge of the basal cavity, which is characteristic of some compressed elements of *C. intermedius*. Another form of compressed element of *C. intermedius* was described as the form-species *Cordylodus prion*; its basal cavity has a convex anterior edge of the basal cavity. It is possible that

these two forms represent distinct species that were associated with such rounded elements as that of *C. intermedius*.

Various authors have interpreted rounded elements of *C. intermedius* differently. Lindström (1955) placed these forms in synonymy with *C. angulatus*. Druce and Jones (1971) pointed out the evolutionary significance of the species and removed it from synonymy with *C. angulatus*. They also described *C. caseyi*, which has a basal cavity similar to that of *C. intermedius* but has an expanded base and long slender cusp. These differences do not seem to be sufficient to recognize a distinct species, and *C. caseyi* is considered here to be a junior subjective synonym of *C. intermedius*. Elements illustrated as *Cordylodus* cf. *C. angulatus* by Druce and Jones (1971) are considered to represent advanced forms of *C. intermedius*.

Müller (1973) described *C. lenzi*, a form-species that has a basal cavity similar to the rounded element of *C. intermedius*. The distinctive feature of *C. lenzi* is a ridge or carina on the anterior part of the cusp. Study of large collections of rounded elements of *C. proavus* and *C. intermedius* reveals that such a ridge is seen on elements of both. This ridge is considered to represent an unimportant morphological variation, and based on the shape of its basal cavity, *C. lenzi* is placed in synonymy with *C. intermedius*.

Occurrence.—*C. intermedius* is widely distributed. In the United States it is known from the Upper Mississippi Valley (Blue Earth beds; Furnish, 1938), Utah (lower House Limestone, House Range; Miller, 1978; Garden City Limestone, Wasatch Range; Mason, 1975), Wyoming-Montana (Bighorn Mountains; Kurtz, 1978), Oklahoma (upper Signal Mountain and lower McKenzie Hill limestones, Wichita Mountains), and Texas (upper San Saba Member of Wilberns Formation and lower Threadgill Member of Tanyard Formation, Llano uplift). All occurrences are in the lower to middle *Symphysurina* Zone or upper Fauna A and lower Fauna B of Ethington and Clark (1971). The lowest occurrences of the species are in Utah in the upper part of the *Cordylodus proavus* Zone (Miller, 1978, table 2). Elsewhere the species is known from Sweden (upper Tremadocian; Van Wamel, 1974), east Baltic region (Viira, 1974), Oaxaca, Mexico (Tiñu Formation; Miller, Robison, & Clark, 1974), Iran (Müller, 1973), Australia (Druce & Jones, 1971; Jones, 1971), northwestern Greenland (Stouge, 1977); and the Soviet Union (Abaimova, 1972, 1975).

CORDYLODUS LINDSTROMI
Druce and Jones

Figure 4I, J; Plate 1, figures 18, 19

Cordylodus lindstromi Druce and Jones, 1971, p. 68, text-fig. 23h, pl. 1, figs. 7-9, pl. 2, fig. 8; Jones, 1971, p. 47, pl. 2, fig. 4; Müller, 1973, p. 32, text-figs. 2D, 6, pl. 9, figs. 10, 11.

Cordylodus angulatus Lindström (part), 1955, p. 551, text-fig. 3E (*not* fig. 3G), ?*not* pl. 5, fig. 9.

Cyrtoniodus prion Miller (part), 1971, p. 79, pl. 1, fig. 17 (*not* figs. 14-16).

Emended description.—Rounded and compressed elements with distinctive basal cavities, secondary apex in cavity extending into first, and rarely second, denticle. Both elements symmetrical and lacking bulge (carina) on either side of posterior process.

Discussion.—Müller (1973) noted that secondary basal cavity tips of the type characteristic of *C. lindstromi* are present in elements of several form-species, including *C. proavus*, *C. prion*, and *C. angulatus*, and concluded that this may not be a reliable species character. However, in multielement taxonomy the first two species of Müller's list represent the rounded and compressed elements, respectively, of *C. lindstromi*, and these elements constitute a distinctive apparatus. Müller's reference to a secondary basal cavity in *C. angulatus* apparently refers to an element illustrated by Druce and Jones (1971, text-fig. 23u), which has a secondary apex anterior rather than posterior to the main apex of the basal cavity. This unique element is considered here to be a variant of *C. angulatus*. In measured sections in Utah, Texas, and Oklahoma compressed and rounded elements of *C. lindstromi* first occur at similar horizons and commonly are found together. These elements are characteristic of the lower part of Fauna B and represent a species easily recognized by the shape of its

basal cavity.

Cordylodus lindstromi apparently evolved from *C. proavus* and seems to have been an evolutionary dead-end.

A single element of *C. oklahomensis* (herein regarded as the compressed element of *C. proavus*) illustrated by Miller (1969, pl. 65, figs. 52, 53) was assigned to *C. lindstromi* by Jones (1971) because of apparent secondary extensions of the basal cavity into several denticles. Subsequent study of this element does not confirm this assignment. The apparent extensions of the basal cavity are quite different from those of *C. lindstromi*, which occurs more than 30 m above the occurrence of this figured element. No similar elements have been found, and the origin of the basal cavity in this specimen is not understood. Possibly it represents a burrow of the type discussed by Müller and Nogami (1972).

Occurrence.—*C. lindstromi* is a widely distributed species. In North America it is known from Utah (lower House Limestone, House Range; lower Garden City Limestone, Wasatch Range; Mason, 1975), Nevada (Whipple Cave Formation, southern Egan Range), Wyoming- Montana (Bighorn Mountains; Kurtz, 1976), Oklahoma (upper Signal Mountain and lower McKenzie Hill limestones, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation and lower Threadgill Member of Tanyard Formation, Llano uplift), eastern New York (Landing, 1976b), Oaxaca, Mexico (Tiñu Formation; Miller, Robison, & Clark, 1974), and the Upper Mississippi Valley (Blue Earth beds, unfigured specimen in collection of Furnish, 1938; illustrated by Miller, 1970).

Several of these North American occurrences are associated with trilobites. *C. lindstromi* first occurs at the base of conodont Fauna B (Ethington & Clark, 1971), which is within the lower part of the *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone. The uppermost occurrence of the species is within the *Symphysurina* Zone. In Mexico *C. lindstromi* is associated with Lower Tremadocian trilobites.

Elsewhere *C. lindstromi* is known from Greenland (Stouge, 1977; Miller & Kurtz, 1979), Sweden (Upper Tremadocian; Lindström, 1955), Australia (Datsonian and Warrendian stages; Druce & Jones, 1971; Jones, 1971), and Iran (Müller, 1973).

With such wide distribution, *C. lindstromi* is an important index fossil. It is most common in the lower part of Fauna B (Ethington & Clark, 1971), but also occurs in the middle of Fauna B, where it is associated with *C. angulatus* and *C. rotundatus*. Although *C. lindstromi* commonly is found in Lower Tremadocian strata, it is not common in the Upper Tremadocian.

CORDYLODUS PROAVUS Müller

Figure 4G, H; Plate 1, figures 14, 15

Cordylodus proavus Müller, 1959, p. 448, text-fig. 3B, pl. 15, figs. 11, 12, 18; 1973, p. 35, text-figs. 2A, 9, pl. 9, figs. 1-9; Miller, 1969, p. 424, text-fig. 3D, pl. 65, figs. 37-45; 1971, p. 79, figs. 18, 19; Ethington and Clark, 1971, pl. 1, fig. 19; Druce and Jones (part), 1971, p. 70 (*not* text-fig. 23p), pl. 1, figs. 2-6 (*not* fig. 1); Jones, 1971, p. 48, pl. 2, fig. 9; Abaimova, 1972, text-fig. 1; 1975, p. 109, text-figs. 8.27, 8.28, pl. 10, fig. 16; Abaimova and Markov, 1977, p. 91, pl. 14, fig. 1; Landing, Taylor, and Erdtmann, 1978, text-fig. 2F; Fåhraeus and Nowlan, 1978, p. 453, pl. 1, figs. 8, 9; Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, figs. 8, 9.

Cordylodus cf. *C. proavus* Druce and Jones, 1971, p. 71, text-fig. 23s, pl. 1, figs. 10, ?11, 12; Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, fig. 10.

Cordylodus oklahomensis Müller, 1959, p. 447, text-fig. 3A, pl. 15, figs. 15, 16; 1973, p. 33, text-figs. 2B, 7, pl. 9, figs. 12, 13; Miller, 1969, p. 423, text-fig. 3I, pl. 65, figs. 46-53; Ethington and Clark, 1971, pl. 1, fig. 24; *not* Druce and Jones, 1971, p. 69, text-fig. 23j, pl. 5, figs. 6, 7; ?*not* Jones, 1971, p. 47, pl. 2, figs. 5-8; Abaimova, 1975, pl. 10, fig. 7.

Cordylodus angulatus Van Wamel (part), 1974, pl. 1, fig. 5 (*not* figs. 6, 7).

Emended description.—Both elements with distinctive basal cavities that have anterior edge essentially paralleling convex anterior edge of element; tips of basal cavities

usually higher than base of most anterior denticle. Rounded element usually symmetrical but may have denticles pointing laterally; cusp and denticles round or oval in cross section, composed of white matter; denticle(s) usually on posterior process but may arise from posterior edge of base in primitive elements; denticles separated at bases. Compressed element asymmetrical due to lateral bending of cusp and to bulge (carina) near base on inner side; cusp and denticles laterally compressed, with sharp edges, and composed of white matter; denticles usually arising from posterior process and fused at bases.

Discussion.—The rounded element of this apparatus is the form-species *C. proavus* and the compressed element is the form-species *C. oklahomensis*. They are here synonymized under the name of the rounded element, which is usually two to four times as abundant as the compressed element. One rounded element and two compressed elements illustrated as *C. proavus* by Druce and Jones (1971, text-fig. 23p, pl. 1, fig. 1; and text-fig. 23j, pl. 5, figs. 6, 7, respectively) are here referred to *C. intermedius*.

Cordylodus proavus can be distinguished from other species of the genus by shape of the basal cavity. In rounded elements of *C. proavus* the anterior edge of the basal cavity curves convexly, whereas in *C. angulatus*, *C. drucei*, *C. intermedius*, and *C. rotundatus* the curve is concave. In *C. lindstromi* the basal cavities of both elements have extensions into the first denticle. The compressed elements of *C. proavus* generally have deeper basal cavities, more strongly developed lateral bulges on one side, and more lateral bending of the cusp compared with compressed elements of other species of *Cordylodus*.

Occurrence.—C. proavus is a cosmopolitan species in faunas of highest Cambrian (*Corbinia apopsis* Subzone of *Saukia* Zone) and lowest Ordovician (*Missisquoia* and lower *Symphysurina* zones) strata. In North America it occurs in the *Cordylodus proavus* Zone of Miller (1978) and in Fauna B of Ethington and Clark (1971). Specific occurrences in the United States include Utah (upper Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (upper Whipple Cave Formation and lower House Limestone, southern Egan Range; upper Hales Limestone, Hot Creek Range), Oklahoma (Signal Mountain Limestone, Arbuckle Mountains (Müller, 1959) and Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation), Wisconsin (Miller, 1971), South Dakota (upper Deadwood Formation, Black Hills), Wyoming-Montana (Kurtz, 1976), Pennsylvania-Maryland (Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), New York (Taconic allochthon; Landing 1976b), and Vermont (Gorge Formation; Landing, 1978). Elsewhere *C. proavus* occurs in East Greenland (upper Dolomite Point Formation; Miller & Kurtz, 1979), New Brunswick, Canada (Landing, Taylor, & Erdtmann, 1978), Alberta, Canada (Derby, Lane, & Norford, 1972), District of Mackenzie, Canada (Tipnis, Chatterton, & Ludvigsen, 1978), Oaxaca, Mexico (Robison & Pantoja-Alor, 1968), Australia (Datsonian Stage; Druce & Jones, 1971; Jones, 1971; Shergold & Druce, 1971), Sweden (upper Tremadocian; Van Wamel, 1974), Soviet Union (Abaimova, 1971, 1975; Abaimova & Markov, 1977), and Iran (Müller, 1973).

CORDYLODUS ROTUNDATUS Pander

Figure 4P; Plate 1, figure 24

Cordylodus rotundatus Pander, 1856, p. 33, pl. 2, figs. 32, 33; Lindström, 1955, p. 533, text-fig. 3F, pl. 5, figs. 17-20; Mound, 1968, p. 409, pl. 2, figs. 4, 5; Druce and Jones, 1971, p. 71, text-fig. 23F, pl. 3, figs. 8-10; Jones, 1971, p. 49, pl. 2, figs. 10, 11; Ethington and Clark, 1971, text-fig. 2, pl. 1, fig. 17; Müller, 1973, p. 36, text-figs. 2H, 10, pl. 11, figs. 8-10; Van Wamel, 1974, p. 60, pl. 1, fig. 14; Viira, 1974, text-fig. 4E, pl. 1, figs. 4, 5, 9, 10.

Cordylodus subangulatus Furnish, 1938, p. 337, text-fig. 2D, pl. 42, fig. 32; Abaimova, 1972, text-fig. 1; Abaimova, 1975, p. 110, text-figs. 29-31, 36, 37, pl. 10, figs. 6, 8, 9, 11.

(In part) *Cordylodus prion* Lindström, 1955, p. 552, pl. 5, figs. 14-16; Druce and Jones, 1971, p. 70, text-fig. 23i, k-o, pl. 2, figs. 1-7; Müller, 1973, p. 33, text-fig. 2E, 8, pl.

10, fig. 4; *not* Van Wamel, 1974, p. 59, pl. 1, figs. 8-9; ?Viira (part), 1974, p. 63, pl. 1, fig. 7 (*not* fig. 6).

(In part) *Cyrtoniodus prion* Ethington and Clark, 1971, pl. 1, fig. 21; Miller, 1971, p. 79, pl. 1, figs. 14-16 (*not* fig. 17).

Emended description.—Distinctive rounded element with anterior edge of basal cavity concavely curved and tip recurved; anterobasal margin well rounded; prominent bulge (carina) near posterior end of one side of denticulate process; basal margin usually arched near middle.

Less distinctive compressed element usually symmetrical or nearly so, with long posterior denticulate process; cusp and denticles compressed laterally and possessing sharp edges; denticles fused at bases. Cusp may be bent slightly to one side and in primitive elements slight bulge (carina) may exist on concave (inner) side near basal margin. Basal cavity moderately deep to shallow, usually extending to near top of posterior process. Anterior edge of basal cavity usually convexly curved but may be concavely curved in some specimens. Compressed elements less abundant than rounded elements, and may be lacking in upper part of species range.

Discussion.—The rounded element of this apparatus is the form-species *C. rotundatus* and the compressed element is the form-species *C. prion*. The same compressed element is believed to have been a part of the apparatuses of *C. angulatus*, *C. drucei*, and *C. intermedius*. Loss of the compressed element in the apparatus of *C rotundatus* and the possibility of an apparatus that included elements of the form-species *C. rotundatus* and *C. angulatus* are discussed under the latter species. Criteria for distinguishing *C. rotundatus* from its ancestor, *C. drucei*, are given under the latter species.

Occurrence.—*C. rotundatus* is a widely distributed species. In the United States it is known in Fauna B (except lower part) and Fauna C. from the Upper Mississippi Valley (Prairie du Chien Group; Furnish, 1938), Colorado (Manitou Formation; Ethington & Clark, 1971), Wyoming-Montana (Bighorn Mountains; Kurtz, 1976), Utah (House Limestone, House Range; Ethington & Clark, 1971; and Garden City Formation, Wasatch Range; Mason, 1975), Oklahoma (upper Signal Mountain and lower McKenzie Hill limestones, Wichita Mountains; and Cool Creek Limestone, Arbuckle Mountains; Mound, 1968), Texas (upper San Saba Member of Wilberns Formation and lower Threadgill Member of Tanyard Formation, Llano uplift), and New York (Taconic allochthon; Landing, 1976b). In other areas *C. rotundatus* has been found in East Greenland (basal Cass Fjord Formation; Miller & Kurtz, 1979), Soviet Union (Pander, 1856; Viira, 1974; Abaimova, 1972, 1975); Iran (Müller, 1973), and Australia (Druce & Jones, 1971; Jones, 1971).

Genus EOCONODONTUS, new

Type species.—*Proconodontus notchpeakensis* Miller, 1969, p. 438.

Description.—Two-element apparatus, rounded and compressed elements lacking posterior process and secondary denticles. Both elements proclined to erect; basal cavities large, moderately to very deep; cusp very short to long and composed of white matter; surface of elements smooth, even at high magnification. More distinctive compressed element asymmetrical due to lateral bending of cusp and to carina on inner side; cusp strongly compressed laterally; anterior and posterior keels or sharp edges prominent. Rounded element less distinctive, lacking carina, and usually symmetrical; anterior and posterior keels prominent in primitive elements, absent in more advanced elements, resulting in oval cross section. Rounded element usually at least two to three times as abundant as compressed element.

Discussion.—Evolutionary relationships among *Proconodontus* Miller, *Eoconodontus*, n. gen., *Cambrooistodus*, n. gen., and *Cordylodus* Pander are discussed in the section on evolution. *Eoconodontus* differs from *Proconodontus* in having two elements instead of one, in having a shorter basal cavity, and in having white matter in the cusp. *Eoconodontus* differs from *Cambrooistodus* by lack of a posterior process on the compressed element. *Cordylodus* differs from all of the above in possessing secondary denticles.

EOCONODONTUS NOTCHPEAKENSIS (Miller)

Figures 3D, E; Plate 1, figures 10-12

Proconodontus notchpeakensis Miller, 1969, p. 438, text-fig. 5G, pl. 66, figs. 21-29; 1971, text-fig. 17N, pl. 2, figs. 19, 20; Lindström, 1973, p. 402, 403, 411; Müller, 1973, p. 43, pl. 4, fig. 6; Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, fig. 14, ?15.

Proconodontus carinatus Miller, 1969, p. 437, text-fig. 5I, pl. 66, figs. 13-20; Lindström, 1973, p. 401-403; Landing, Taylor, and Erdtmann, 1978, text-fig. 2A.

Oneotodus nakamurai Nogami (part), 1966, p. 216, text-figs. 3D, E (*not* text-figs. 3A-C), pl. 1, figs. 10, 11 (*not* figs. 9, 12, 13); ?Druce and Jones (part), 1971, p. 82, text- fig. 23j (*not* text-fig. 23i), pl. 10, figs. 1, 2, 5, 6 (*not* figs. 3, 4, 7, 8); ?Jones (part), 1971, p. 58, pl. 4, figs. 1, 3 (*not* figs. 2, 4); Lee, 1975, p. 81, text-figs. 2E, G, pl. 1, figs. 6, 9, 10; Abaimova and Markov, 1977, p. 92, pl. 14, figs. 12-14, 16.

Proconodontus mülleri mülleri [sic] Özgül and Gedik, 1973, p. 49, pl. 1, fig. 6.

Proconodontus sp. aff. *P. carinatus* Özgül and Gedik, 1973, p. 49, pl. 1, fig. 15.

?*Oneotodus altus* Viira, 1970, text-fig. 7, pl. 10, fig. 7.

Description.—Because the genus is monotypic, the species description is the same as that for the genus.

Discussion.—Nogami (1966) assigned elements with both round and oval cross sections to *Oneotodus nakamurai.* Miller (1969) assigned only those elements with round cross sections to *O. nakamurai;* these elements are reassigned herein to *Teridontus nakamurai.* Miller (1969) assigned Nogami's elements with oval cross sections to *Proconodontus notchpeakensis.* Druce and Jones (1971), Jones (1971), Lee (1975), and Abaimova and Markov (1977) followed Nogami in assigning some elements with oval cross sections to *O. nakamurai.* These elements are herein considered to be rounded elements of *Eoconodontus notchpeakensis,* but compressed elements of the same apparatus do not appear to have been illustrated. Nevertheless, my reference collections from the Black Mountain section of Druce and Jones (1971) contain both rounded and compressed elements of *E. notchpeakensis,* although they are much rarer than elements of *"Oneotodus" nakamurai.* Further testing of the correct assignment of Australasian elements assigned to *"O." nakamurai* is possible by utilizing a scanning electron microscope to search for microstriae on the elements. *Eoconodontus* elements are smooth, whereas elements of *"O." nakamurai* have fine striae visible at high magnification.

I questionably reassign to *E. notchpeakensis* two elements assigned by Jones (1971, pl. 4, figs. 1, 3) to *Oneotodus nakamurai.* These may instead be broken *Cordylodus* elements.

Two elements from Turkey are reassigned to *E. notchpeakensis.* The element assigned to *Proconodontus mülleri mülleri* [sic] by Özgül and Gedik (1973, pl. 1, fig. 6) has a tip composed of white matter and the short basal cavity is characteristic of the rounded element of *E. notchpeakensis.* The element identified as *Proconodontus* sp. aff. *P. carinatus* by Özgül and Gedik (1973, pl. 1, fig. 15) is the compressed element of the *E. notchpeakensis* apparatus.

Oneotodus altus Viira (1970) is a questionable synonym of this species.

Occurrence.—*E. notchpeakensis* is cosmopolitan, being present in most latest Cambrian and earliest Ordovician conodont faunas. In North America it occurs with well-studied trilobite faunas, and its range is from near the middle of the *Saukiella junia* Subzone of the *Saukia* Zone (middle Trempealeauan) well into the Lower Ordovician *Symphysurina* Zone. In the United States *E. notchpeakensis* is known from Utah (Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (Whipple Cave and lower House limestones, southern Egan Range; Hales Limestone, Hot Creek Range), Wyoming-Montana (Bighorn Mountains; Kurtz, 1976), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), Wisconsin (Lodi Siltstone; Miller, 1971), and Pennsylvania-Maryland (Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972). Elsewhere *E. notchpeakensis* is known from Alberta,

Canada (upper Mistaya and lower Survey Peak formations; Derby, Lane, & Norford, 1972); District of Mackenzie, Canada (Rabbitkettle Formation; Tipnis, Chatterton, & Ludvigsen, 1978), western North Greenland (upper Cass Fjord Formation; Kurtz, 1977), East Greenland (upper Dolomite Point and lower Cass Fjord formations; Miller & Kurtz, 1979), China (Nogami, 1966), South Korea (Lee, 1975), Soviet Union (Abaimova & Markov, 1977), Iran (Müller, 1973), Turkey (Özgül & Gedik, 1973), and Australia (Druce & Jones, 1971; possibly Jones, 1971).

Genus FRYXELLODONTUS Miller, 1969

Type species.—*Fryxellodontus inornatus* Miller, 1969, p. 426; by original designation.

Discussion.—Miller (1969) described two species of this genus, *Fryxellodontus inornatus* and *F. lineatus*, from Utah. Serpagli (1974, p. 47) described *Fryxellodontus? corbatoi* from the Lower Ordovician of Argentina, and Landing (1976c, p. 632) described *Fryxellodontus? ruedemanni* from approximately coeval strata in New York. The latter two species appear to be related to each other, but their morphology and ornamentation are quite different from the former two. Similarities of apparatus plan in all of these species may indicate a relationship; however, the species of Serpagli (1974) and Landing (1976c) are considerably younger than the Utah species. As Landing (1976c, p. 633) pointed out, the inclusion of *F.? corbatoi* and *F.? ruedemanni* within *Fryxellodontus* considerably expands the concept of the genus and its stratigraphic range. *F.? corbatoi* and *F.? ruedemanni* are here considered to be related species of an undescribed genus.

FRYXELLODONTUS INORNATUS Miller

Figure 5A-D

Fryxellodontus inornatus Miller (part), 1969, p. 426, text-figs. 4A, C-E, pl. 65, figs. 1-10, 12-16, 23-25 (*not* fig. 11); Lindström, 1973, p. 79-81.

Gen. et sp. indet. B Druce and Jones, 1971, p. 102, text-fig. 33, pl. 12, fig. 9.

Discussion.—Lindström (1973, p. 79) pointed out that holotypes were incorrectly designated for each of the four elements of this species. To insure taxonomic stability of the species, I here designate one planar element from the type-series (Miller, 1969, pl. 65, figs. 1-3; UW 1309) as lectotype. One paratype, a serrate element (Miller, 1969, pl. 1, fig. 11), is here reassigned to *F. lineatus* on the basis of its ornamentation.

Occurrence.—*F. inornatus* is known in North America from Utah (upper Notch Peak and basal House limestones, House Range; Miller, 1969, 1978), Nevada (Hales Limestone, Hot Creek Range; Whipple Cave Formation, southern Egan Range), South Dakota (upper Deadwood Formation, Black Hills), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), Alberta, Canada (Survey Peak Formation; Derby, Lane, & Norford, 1972), and from the eastern Canadian Arctic Islands (Nowlan & Barnes, 1976). Elsewhere the species is known from East Greenland (upper Dolomite Point Formation; Miller & Kurtz, 1979) and Australia (Druce & Jones, 1971).

Fryxellodontus inornatus first appears precisely at the base of the *Missisquoia typicalis* Subzone of the *Missisquoia* Zone of Stitt (1977), and ranges through the remainder of the zone and into the lower part of the *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone (Stitt, 1977). With this short stratigraphic range, the species is an excellent index fossil, ranging only from the base of the *Fryxellodontus inornatus* Subzone to the base of the *Hirsutodontus simplex* Subzone of the *Cordylodus proavus* Zone (Fig. 1).

FRYXELLODONTUS LINEATUS Miller

Fryxellodontus lineatus Miller, 1969, p. 429, text-figs. 4B, F, p. 65, figs. 17-22, 26-29; Lindström, 1973, p. 80-83.

Fryxellodontus inornatus Miller (part), 1969, p. 426, pl. 65, fig. 11 (*not* figs. 1-10, 12-16, 23-25).

Discussion—As with *F. inornatus*, "holotypes" were incorrectly designated for each of three elements of *F. lineatus*. To insure tax-

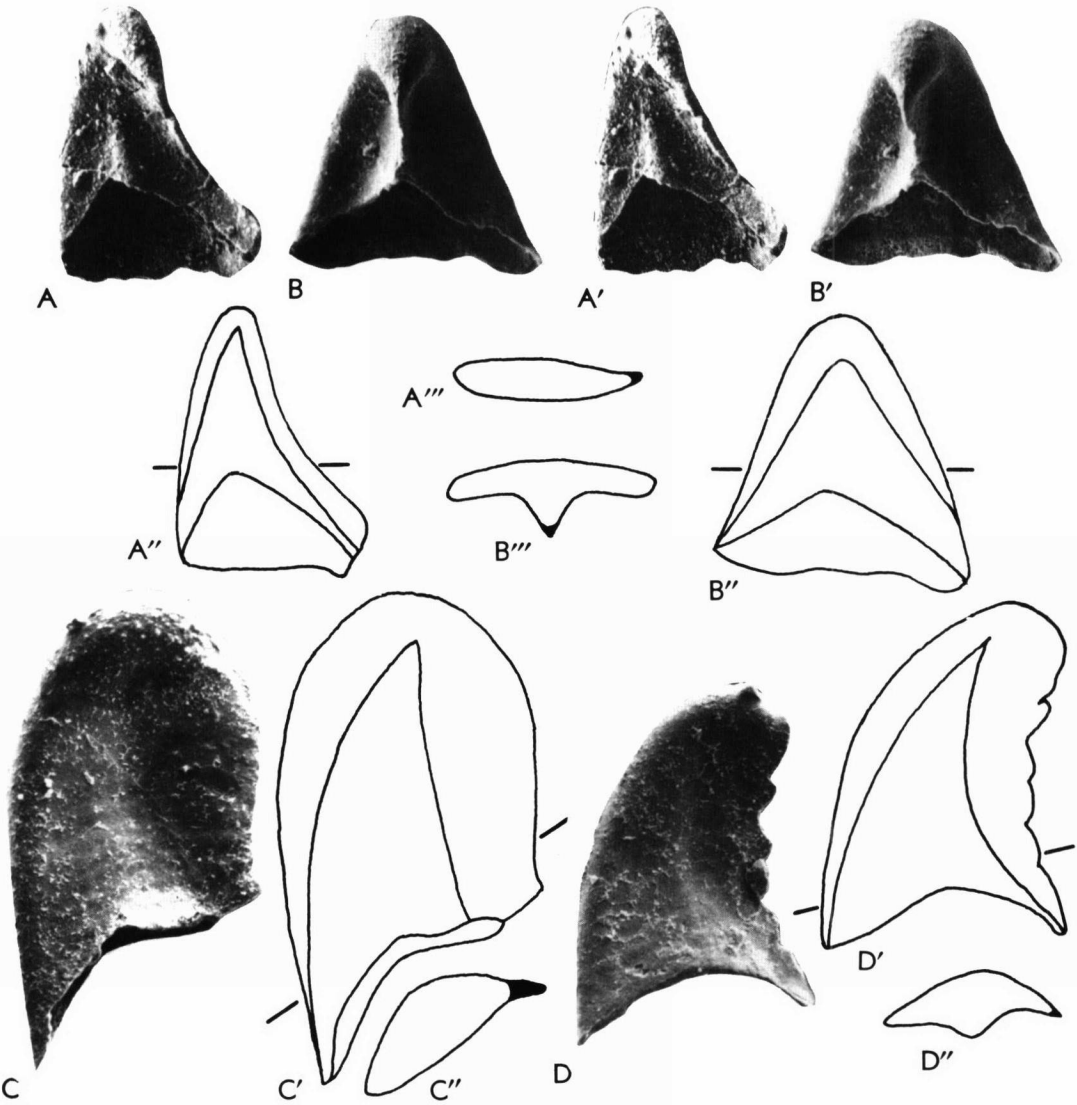

Fig. 5. Elements of *Fryxellodontus inornatus* Miller with line drawings of basal cavities and transverse sections; all from Signal Mountain Limestone, Wichita Mountains, Oklahoma; 472 m (1,546 ft) above base of Chandler Creek section of Stitt (1977).——A. Lateral stereophotos (A,A′) and drawings (A″,A‴) of planar element, USNM 303410.——B. Lateral stereophotos (B,B′) and drawings (B″,B‴) of serrate element, USNM 303411.——C. Lateral view (C) and drawings (C′,C″) of intermediate element (posterior), USNM 303412.——D. Lateral view (D) and drawings (D′,D″) of symmetrical element (posterior), USNM 303413. Black area on each transverse section shows position of prominent ridge. All X120.

onomic stability of the species, I here designate one intermediate element from the type-series (Miller, 1969, pl. 65, figs. 17-19, UW 1306) as a lectotype.

When I described this species only the symmetrical, intermediate, and serrate elements were known, but I have subsequently discovered planar elements with the characteristic linear ornamentation of this species. This element is found throughout the *Fryxellodontus inornatus* and *Clavohamulus elongatus* Subzones of the *Cordylodus pro-*

avus Zone (Fig. 1), whereas the other elements occur only from the base of the *C. elongatus* Subzone to the base of the overlying *Hirsutodontus simplex* Subzone.

Lindström (1973, p. 79, 83) suggested that *F. lineatus* might be a junior synonym of *F. inornatus;* however, after studying much new material, I am convinced that both species warrant recognition. Besides having distinctive linear ornamentation, most of the elements of the *F. lineatus* apparatus have a shorter stratigraphic range than do those of *F. inornatus.* Also, the apparatus of *F. lineatus* has a smaller proportion of planar and serrate elements.

Occurrence.—F. lineatus occurs only in the United States, where it is known from Utah (upper Notch Peak and House limestones, House Range; Miller, 1969, 1978), South Dakota (upper Deadwood Formation, Black Hills), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), New York (upper Whitehall Formation; J. E. Repetski, pers. commun.), and Missouri (upper Eminence Dolomite; V. E. Kurtz, pers. commun.).

Genus HIRSUTODONTUS Miller, 1969

Type species.—Hirsutodontus hirsutus Miller, 1969, p. 431; by original designation.

Discussion.—I follow Jones (1971, p. 56) and consider *Strigaconus* Druce and Jones, 1971, to be a junior subjective synonym of *Hirsutodontus* Miller, 1969. The apparatus of *Hirsutodontus* consists of one form of element.

HIRSUTODONTUS HIRSUTUS Miller

Figure 4N; Plate 2, figure 14

Hirsutodontus hirsutus Miller (part), 1969, p. 431, text-fig. 4I, pl. 64, figs. 25, 26, 29-31 (*not* figs. 27, 28, 32-35); *not* Jones, 1971, p. 56, pl. 7, figs. 7, 8; Lindström (part), 1973, p. 119.2, 121 (*not* p. 119.3).

Emended diagnosis.—Ornamentation consisting of small nodes, large spines lacking.

Discussion.—Species of *Hirsutodontus* can be distinguished from each other by differences in cusp length and ornamentation. *H. hirsutus* has a well-developed cusp and small nodes, whereas *H. simplex* has much larger spines. *H. rarus* has many tiny spines and a poorly developed cusp. *H. lenaensis* has small nodes distributed over all of the small, blunt cusp and is most similar to *H. hirsutus,* which differs by usually lacking nodes on the posterior.

Jones (1971) and Lindström (1973) synonymized *Strigaconus simplex* Druce and Jones, 1971, with *Hirsutodontus hirsutus* Miller, 1969; however, E. C. Druce and I jointly realized that although the genera are synonyms, holotypes of the respective species are not elements of the same species. The nodose *H. hirsutus* occurs throughout the *Cordylodus proavus* Zone in the United States, whereas the spiny *H. simplex* is found only in the two upper subzones of the *C. proavus* Zone (Miller, 1978). Accordingly, spinose elements figured by Miller (1969, pl. 64, figs. 27, 28, 32-35), Jones (1971, pl. 7, figs. 7, 8) and Lindström (1973, p. 119.3), which were assigned to *H. hirsutus,* are reassigned to *H. simplex.*

Occurrence.—H. hirsutus, as emended, occurs only in North America, and is known in Utah (upper Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range), South Dakota (upper Deadwood Formation, Black Hills), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), New York (upper Whitehall Formation; J. E. Repetski, pers. commun.), and Alberta, Canada (Survey Peak Formation; Derby, Lane, & Norford, 1972).

HIRSUTODONTUS LENAENSIS Abaimova

Hirsutodontus(?) lenaensis Abaimova, 1971, p. 79, text-fig. 5, pl. 10, fig. 11; 1972, text-fig. 1; 1975, p. 73, text-fig. 7.4, 7.5, pl. 6, figs. 1-3; Lindström, 1973, p. 118, 119.4, 123.

Discussion.—I have not seen elements of *Hirsutodontus lenaensis,* but illustrations show them to be morphologically distinct (see discussion under *H. hirsutus*). The species is

known only from the Lower Ordovician of the Soviet Union in strata much younger than those with other species of *Hirsutodontus* (Abaimova, 1972).

HIRSUTODONTUS RARUS Miller

Plate 2, figure 3

Hirsutodontus rarus Miller, 1969, p. 431, text-fig. 4H, pl. 64, figs. 36-42; Abaimova, 1972, text-fig. 1; 1975, p. 72, text-fig. 7.10, pl. 1, fig. 20; Lindström, 1973, p. 118, 119, 125; Abaimova and Markov, 1977, p. 91, pl. 14, figs. 4, 7, pl. 15, fig. 5.

Discussion.—*H. rarus* apparently evolved from *H. hirsutus* and differs in having a shallower basal cavity, a more poorly developed cusp, and much smaller and more closely spaced spines. *Clavohamulus elongatus*, an evolutionary descendant of *H. rarus*, has granulose ornamentation and virtually neither cusp nor basal cavity.

Occurrence.—In the United States, *Hirsutodontus rarus* is known from throughout the *Cordylodus proavus* Zone of Utah (upper Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), and Texas (upper San Saba Member of Wilberns Formation, Llano uplift). Elsewhere *H. rarus* is known from East Greenland (upper Dolomite Point Formation; Miller & Kurtz, 1979), the Soviet Union (Abaimova, 1972, 1975), and Australia (E. C. Druce, pers. commun., 1979).

HIRSUTODONTUS SIMPLEX (Druce & Jones)

Figure 4S; Plate 2, figure 13

Strigaconus simplex Druce and Jones, 1971, p. 98, text-fig. 31, pl. 6, figs. 1-5.

Hirsutodontus hirsutus Miller (part), 1969, p. 431, pl. 64, figs. 27, 28, 32-35 (*not* figs. 25, 26, 29-31); Jones, 1971, p. 56, pl. 7, figs. 7, 8; Lindström (part), 1973, p. 118, 119.3, 121 (*not* 119.2).

Hirsutodontus dzherbiensis Abaimova, 1971, p. 79, text-fig. 4, pl. 10, figs. 9, 10; 1972, text- fig. 1; 1975, p. 71, text-fig. 7.11, p. 6, figs. 7, 8; Abaimova and Markov, 1977, p. 91, pl. 14, figs. 8, 9, p. 15, figs. 2, 6, 7.

Hirsutodontus cf. *H. hirsutus* Abaimova and Markov, 1977, p. 92, pl. 14, fig. 10.

Discussion.—The relationship between *H. simplex* and *H. hirsutus* is discussed under the latter species.

Hirsutodontus dzherbiensis Abaimova, 1971, is a large-spined form that Lindström (1973, p. 121) synonymized with *H. hirsutus;* however, it is here considered to be a junior synonym of *H. simplex* (Druce & Jones), 1971. Druce and Jones' (1971) publication was issued May 15, 1971, while Abaimova's (1971) paper is in the October-December, 1971, issue of the Paleontologicheskiy Zhurnal.

Occurrence.—*H. simplex* is known in North America from Utah (lower House Limestone, House Range; Miller, 1969, 1978), Nevada (Hales Limestone, Hot Creek Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), and Texas (upper San Saba Member of Wilberns Formation, Llano uplift). Elsewhere it is known in Australia (Druce & Jones, 1971; Jones, 1971) and the Soviet Union (Abaimova, 1971, 1972, 1975; Abaimova & Markov, 1977). In the United States *H. simplex* ranges through a stratigraphic interval of only about 15 m in a thick miogeosynclinal sequence (Miller, 1978, table 2). This interval is within the lower *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone and in the *Hirsutodontus simplex* and lower *Clavohamulus hintzei* subzones of the *Cordylodus proavus* Zone. The Australian occurrences are likewise confined to a thin interval, making *H. simplex* an excellent index for international correlation.

Genus MONOCOSTODUS, new

Type species.—*Acodus sevierensis* Miller, 1969, p. 418.

Description.—Apparatus consisting of symmetry-transition series with slender, erect to reclined, simple cones; dextral, sinistral, and rare bilaterally symmetrical symmetry-transition variants produced by changes in position of narrow, sharp costa beginning near bend of cusp and extending to tip; costa

usually on right or left side, rarely posterior. Cross section of base and lower cusp round to oval; cusp composed of white matter.

MONOCOSTODUS SEVIERENSIS (Miller)

Figure 4U; Plate 2, figures 8, 9

Acodus sevierensis Miller (part), 1969, p. 418, pl. 63, figs. 25-31 (*not* figs. 21-24, 32).
Acontiodus (Semiacontiodus) unicostatus Miller (part), 1969, p. 421, pl. 64, figs. 49-54 (*not* figs. 46-48).
Drepanodus simplex Druce and Jones, 1971, p. 24, text-fig. 24b, pl. 13, figs. 1-4.
Semiacontiodus sevierensis Lindström, 1973, p. 442-445.

Description—Because the genus is monotypic, the description of the species is the same as that of the genus.

Discussion.—Confusion regarding *Acodus sevierensis*, *Acontiodus (Semiacontiodus) unicostatus*, and *Paltodus utahensis* has resulted from my earlier descriptions (Miller, 1969). These emphasized the number of costae and their symmetrical or asymmetrical disposition on the cusp. The original description of *A. sevierensis* included all unicostate, asymmetrical specimens of two element types. On one type the costa end near the apex of the basal cavity, and on the other type the costa continue to the basal margin. These two element types are now understood to represent two different apparatuses. Elements of the first type, with short costae, are here assigned to *Monocostodus sevierensis*, as are similar rare symmetrical elements with a posterior costa. These elements constitute a simple symmetry series. Elements of the second type, with longer costae, together with some elements formerly assigned to *Acontiodus (Semiacontiodus) unicostatus* Miller, constitute a different apparatus that is here assigned to *Utahconus utahensis* (Miller).

Lindström (1973) reassigned all of the above species to *Semiacontiodus* Miller, 1969; however, the apparatus of *Semiacontiodus* is sufficiently different from those of *Monocostodus* and *Utahconus* that his reassignment is not followed here.

Druce and Jones (1971) assigned Australian elements of this species to *Drepanodus simplex* Branson and Mehl. Those elements appear to be more robust and have more strongly developed costae than most of my *M. sevierensis* elements but fall within the range of variation of the species. Also, they have a stratigraphic range (Druce & Jones, 1971, fig. 15) similar to that of *M. sevierensis* in the western United States. *Drepanodus simplex* is a much younger species described from the Jefferson City Dolomite, which is late Early Ordovician in age. The white matter in *D. simplex* is confined to a growth axis, whereas in *M. sevierensis* the cusp is solid white matter. These two species probably also had different types of apparatuses.

Occurrence.—*M. sevierensis* is known from Utah (top of Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (top of Whipple Cave and lower House limestones, southern Egan Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), Pennsylvania-Maryland (upper Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), and Australia (Druce & Jones, 1971). In the United States the species is found in the lower *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone. *M. sevierensis* occurs in the *Hirsutodontus simplex* and *Clavohamulus hintzei* Subzones of the *Cordylodus proavus* Zone (Miller, 1978, table 2) and in Fauna B of Ethington & Clark (1971).

Genus MUELLERODUS, new

Type species.—*Distacodus(?) cambricus* Müller, 1959, p. 450.

Description.—Proclined to reclined simple-cone paraconodonts; cusp may be bent laterally, tip of cusp may be recurved sigmoidally; base large, basal cavity deep; anterior and posterior edges rounded, lateral faces each with long, prominent costa.

Discussion.—*Muellerodus* is proposed as a replacement for *Muellerina* Szaniawski, 1971, which is a junior homonym of *Muellerina* Bassiouni, 1965, an ostracode. Szaniawski (1971, p. 407) assigned three species to his genus. Clearly, none of the species, which are Cam-

brian paraconodonts, should be assigned to *Distacodus* Hinde, an Ordovician euconodont.

Etymology.—Following the wish of Szaniawski (1971, p. 407) to honor Klaus Müller of the University of Bonn, the name is composed from Müller and a derivative of the Greek *dont*, a tooth.

Genus NERICODUS Lindström, 1955

Type species.—*Nericodus capillamentum* Lindström, 1955, p. 570.

Diagnosis.—Unusual arched simple-cone elements with surface highly modified by unevenly distributed nodes that may be joined to form irregular ridges.

NERICODUS CAPILLAMENTUM Lindström

Figure 6A-C

Nericodus capillamentum Lindström, 1955, p. 570, pl. 6, figs. 41, 42.

Discussion.—The description of this monotypic genus was based on a single specimen that has not been illustrated previously with photographs. Stig Bergström kindly assisted in obtaining the holotype for study and provided the few fragments recovered from his extensive Swedish conodont collections. After studying all of this material with a scanning electron microscope, I conclude that the holotype is broken. Figure 6 includes stereophotos of the upper and lower surfaces of the holotype. It appears that a symmetry plane would divide the specimen into equal right and left sides, except where the left basal corner (process) is broken off. The right side appears to be intact.

The relationship of this unusual element to other genera is unclear. The fragments found by Bergström are sufficiently similar to the holotype that one can rule out the possibility of its being a unique pathologic oddity. The only conodont that approaches the ornamentation of this element is *Hirsutodontus simplex* (Druce & Jones), illustrated on Plate 2, figure 13. Perhaps *N. capillamentum* is related to *H. simplex*.

Genus NOGAMICONUS, new

Type species.—*Proacodus? sinensis* Nogami, 1966, p. 356.

Description.—Simple-cone paraconodonts, asymmetrical, usually occurring as both sinistral and dextral elements; basal cavity large and deep, cusp above basal cavity small or absent; anterior and posterior keels present, with one or more lateral carinae.

Discussion.—Several apparently related species described by Nogami (1966, 1967) from China are assigned to this genus. All have prominent carinae and keels, and it appears useful to group these unusual species within a single genus. These are *Proacodus? sinensis* Nogami (1966, p. 356, pl. 10, figs. 12-14), *Acodus cambricus* Nogami (1967, p. 213, text-figs. 1A, B, pl. 1, figs. 1, 3, 4 only), *Hertzina(?) tricarinata* Nogami (1967, p. 214, text-fig. 2, pl. 6, figs. 5-8), and *Proacodus?* n. sp. Nogami (1966, p. 357, pl. 10, figs. 15, 16).

Etymology.—Named in honor of Yasuo Nogami for his important studies of Cambrian conodont taxonomy and microstructure; *conus* (Latin), a cone.

Genus PROCONODONTUS Miller, 1969

Type species.—*Proconodontus muelleri* Miller, 1969, p. 437; by original designation.

Emended description.—Apparatus containing single type of large, simple-cone element, erect to proclined, usually symmetrical, or may be slightly asymmetrical due to lateral curvature, cross section oval; basal cavity extending to tip, white matter lacking, basal cone prominent; keels on anterior or posterior edge, or both.

Discussion.—The above description restricts this genus to species possessing extremely deep basal cavities and lacking white matter. The form-species *"P." notchpeakensis* and *"P." carinatus* have shorter basal cavities and cusps composed of white matter, and they are reassigned to *Eoconodontus*, n. gen.

Based on stratigraphic position and morphology, *Proconodontus* appears to be one of the most primitive genera of the conodontophorid conodonts (euconodonts). The ancestor of *Proconodontus* is uncertain (see discussion under *P. tenuiserratus*), but the genus is itself the ancestor of an important

lineage of Upper Cambrian and Lower Ordovician conodonts.

PROCONODONTUS MUELLERI Miller

Figure 4C; Plate 1, figure 7

Proconodontus mülleri mülleri [sic] Miller, 1969, p. 437, text-fig. 5H, pl. 66, figs. 30-40; Lindström, 1973, p. 402, 403, 407; *not* Özgül and Gedik, 1973, p. 49, pl. 1, fig. 6.

Proconodontus mulleri mulleri [sic] Ethington and Clark, 1971, pl. 1, fig. 25.

Proconodontus muelleri muelleri Miller, 1971, pl. 2, fig. 18; ?Fåhraeus and Nowlan, 1978, p. 453, pl. 1, figs. 1, 2; Tipnis, Chatterton, and Ludvigsen, 1978, pl. 1, figs. 3, 13, 17.

Coelocerodontus burkei Druce and Jones (part), 1971, text-fig. 22a (*not* text-fig. 22E), pl. 11, figs. 9-11 (*not* figs. 5-8, 12).

?Proconodontus muelleri Müller (part), 1973, p. 42, pl. 3, figs. 4-7, ?10 (*not* fig. 8); Miller and Paden, 1976, p. 595, pl. 1, figs. 4, 5.

Diagnosis.—Both anterior and posterior keels present, latter not serrate; either keel may not extend completely from tip to base.

Discussion.—Druce and Jones (1971) described *Coelocerodontus burkei* from Australia. The holotype (text-fig. 22a, pl. 11, fig. 11) has all of the characteristics of this species, and thus *C. burkei* is judged to be a junior subjective synonym of *Proconodontus muelleri*. Some paratypes of *C. burkei* are judged to represent *P. posterocostatus*, *P. serratus*, and *P. tenuiserratus*.

Some elements from Iran assigned by Müller (1973) to *P. muelleri* appear to be incorrectly identified. Müller's illustrations do

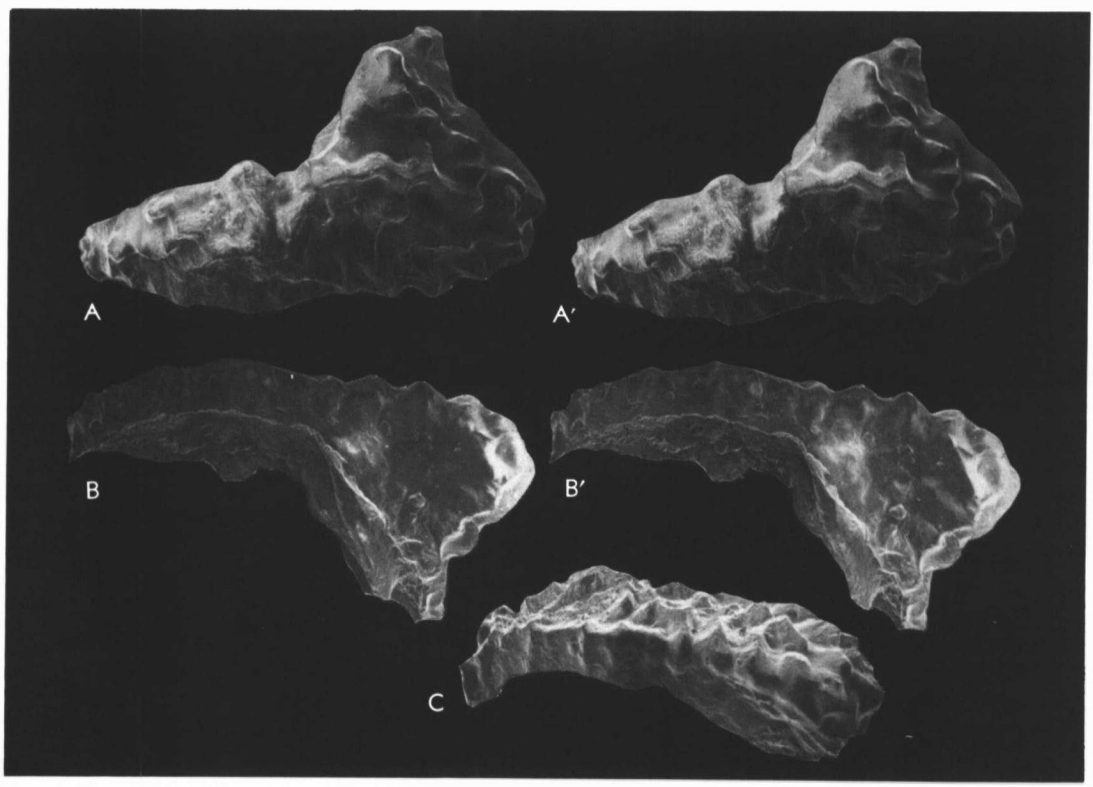

Fig. 6. *Nericodus capillamentum* Lindström; holotype, uncoated.——A,B. Stereophotos of anterior (upper?) and posterior (lower?) surfaces.——C. Lateral view. Tip oriented toward right in all illustrations; all X85.

not show the basal cavities. One of the elements (Müller, 1973, pl. 3, fig. 8) is reassigned to *Eoconodontus notchpeakensis*, and another (pl. 3, fig. 10) may be the same species. Müller's (pl. 3, figs. 4-7) remaining figured elements are not assigned to another species, but I judge that they are not *P. muelleri*. Müller (1973) has identified elements of *P. muelleri* associated with conodont faunal assemblages characteristic of faunas A, B, and C of Ethington and Clark (1971), whereas in the United States *P. muelleri* is not associated with faunas so young. Elements identified by Müller (1973) as *P. muelleri* from strata below Fauna A may be correctly identified, but none is illustrated.

One element assigned to this species by Özgül and Gedik (1973, pl. 1, fig. 6) is here reassigned to *Eoconodontus notchpeakensis* because of basal cavity shape and the white matter in the cusp.

Miller and Paden (1976, pl. 1, figs. 4, 5) assigned to this species two elements from California. The elements are broken, the basal cavities are not illustrated, and the description of the elements is brief. They do not appear to be *P. muelleri*, although I cannot confidently assign them to another species.

In Newfoundland Fåhreaus and Nowlan (1978, text-fig. 4, pl. 1, figs. 1, 2) assigned to *P. muelleri* two specimens that occur with elements of *C. proavus*. Illustrations of these do not show the basal cavities, but they do not appear to be *P. muelleri*. All other occurrences of their *P. muelleri* are from strata below the lowest occurrence of *C. proavus*.

In describing *P. muelleri* (Miller, 1969), I reported its stratigraphic range as overlapping the ranges of *Cordylodus proavus* and species of *Clavohamulus, Hirsutodontus, Oneotodus, Paltodus*, and *Semiacontiodus*. Restudy of original collections shows that all Utah specimens previously identified as *P. muelleri* from within this range are broken elements of *Eoconodontus notchpeakensis*. The correct range of *P. muelleri* and other Utah species was shown by Miller (1978, table 2). *P. muelleri* has not been found associated with *Cordylodus proavus* or younger faunas in Utah, Nevada, Oklahoma, or Texas, although in Texas the ranges of the species are separated by only a bedding plane. The range of *P. muelleri* in these areas is from the upper *Rasettia magna* Subzone to the top of the *Saukiella serotina* Subzone of the *Saukia* Zone (Fig. 1). These strata were assigned to the *Proconodontus* Zone by Miller (1978).

Occurrence.—*P. muelleri* is a widespread species. In the United States it is known from Utah middle and upper Notch Peak Limestone, House Range; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range; upper Catlin and lower Bullwhacker Members of Windfall Formation, Eureka Mining District), Wyoming-Montana (Bighorn Mountains; Kurtz, 1976), Colorado (Manitou Formation; Ethington & Clark, 1971), Oklahoma (Signal Mountain Limestone, Wichita Mountains), Texas (San Saba Member of Wilberns Formation, Llano uplift), and New York (Taconic allochthon; Landing, 1976a). Elsewhere it is known from Alberta, Canada (Survey Peak Formation; Derby, Lane, & Norford, 1972), Arctic Canada (Nowlan & Barnes, 1976); District of Mackenzie, Canada (Rabbitkettle Formation; Tipnis, Chatterton, & Ludvigsen, 1978), Newfoundland, Canada (Fåhraeus & Nowlan, 1978), western North Greenland (Cass Fjord Formation; Kurtz, 1977), Iran (Müller, 1973), and Australia (Druce & Jones, 1971).

PROCONODONTUS POSTEROCOSTATUS, new species

Figure 4B; Plate 1, figures 4-6

Coelocerodontus burkei Druce and Jones (part), 1971, p. 61, pl. 11, figs. 7, 8 (*not* figs. 5, 6, 9-12).

Holotype.—USNM 303275 (Figure 4B; pl. 1, fig. 4).

Description.—Moderate to large simple cones, erect to proclined, symmetrical; cross section round to oval below bottom of posterior keel; white basal cone thick and prominent, accounting for most of mass of element; basal cavity extending nearly to tip of basal cone, which extends to tip of element. Wall covering basal cone usually thin and easily exfoliated; wall extended posteriorly as prominent keel that may be one-third total width of element; keel typically not reaching basal margin. Anterior keel absent.

Discussion.—Two elements assigned to *Coelocerodontus burkei* Druce and Jones

(1971, pl. 11, figs. 7, 8) are reassigned to this species. Other elements of *P. posterocostatus* are in my reference collections from the Black Mountain section of Druce and Jones (1971). Elements from Texas and Australia appear to be indistinguishable.

This primitive euconodont appears to have evolved from *P. tenuiserratus*, n. sp., by enlargement of the small posterior serrate keel. *P. posterocostatus* is the ancestor of *P. muelleri*, which has both anterior and posterior keels.

Occurrence.—*P. posterocostatus* is known from Texas (121 elements from Saba Member of Wilberns Formation, Llano uplift); Oklahoma (seven elements from upper Fort Sill Limestone; Wichita Mountains), and Nevada (one element from upper Catlin Member of Windfall Formation, Eureka Mining District). These elements occur in uppermost Franconian to lower Trempealeauan strata (upper *Ellipsocephaloides* Zone, *Saukiella pyrene* and lower *Saukiella junia* subzones of *Saukia* Zone). The species is also known from Australia (Druce & Jones, 1971).

PROCONODONTUS SERRATUS Miller

Figure 4D; Plate 1, figure 13

Proconodontus mülleri [sic] *serratus* Miller, 1969, p. 438, pl. 66, figs. 41-44; Lindström, 1973, p. 402, 403, 409.

Coelocerodontus burkei Druce and Jones (part), 1971, p. 61, pl. 11, fig. 12 (*not* figs. 5-11).

Proconodontus serratus Müller, 1973, p. 44, pl. 4, figs. 1, 2.

Discussion.—*Proconodontus serratus* is easily recognized by its deep basal cavity, prominent anterior keel, and serrate posterior keel. It probably evolved from *P. muelleri*, and is not a common species.

One paratype of *Coelocerodontus burkei* (Druce & Jones, 1971, pl. 11, fig. 12) is reassigned to this species because of its posterior serrate keel and an anterior keel.

Occurrence.—*P. serratus* is known in North America from Utah (Notch Peak Formation, House Range; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range), Oklahoma (Signal Mountain Limestone, Wichita Mountains), Texas (San Saba Member of Wilberns Formation, Llano uplift), and New York (Taconic allochthon; Landing, 1976a). Elsewhere it is known from Alberta, Canada (base of Survey Peak Formation; Derby, Lane, & Norford, 1972), Australia (Druce & Jones, 1971), and Iran (Müller, 1973). In North America *P. serratus* is associated with trilobites diagnostic of the upper *Saukiella junia* and the *S. serotina* subzones of the *Saukia* Zone (Trempealeauan). It does not extend into the range of *Cordylodus proavus* in North America (Miller, 1978, table 2) or in Australia (Druce & Jones, 1971, text-fig. 18). Müller (1973) reported the species to be associated with *C. proavus*, although his illustrated specimens were from older strata that did not yield *C. proavus*.

PROCONODONTUS TENUISERRATUS, new species

Figure 4A; Plate 1, figures 1-3

Coelocerodontus burkei Druce and Jones (part), 1971, p. 61, text-fig. 22e, pl. 11, figs. 5, 6 (*not* figs. 7-12).

Holotype.—USNM 303277 (Figure 4A; Pl. 1, fig. 2).

Description.—Moderate to small simple cones, erect to proclined, symmetrical; except for small posterior keel, cross section usually round from base to tip, rarely oval near base; white basal cone thick and prominent, accounting for most of mass of element, basal cone extending to tip of element; basal cavity extending nearly to tip of basal cone. Wall covering basal cone thin and usually partly exfoliated near base. Posterior keel small and finely serrate, extending from tip about half way to base; serration visible only under high magnification; anterior keel absent. Elements usually white in color.

Discussion.—*Proconodontus tenuiserratus* is the most primitive species of its genus and one of the most primitive euconodonts. Its morphology suggests a relationship to *Prooneotodus rotundatus* (Druce & Jones), an associated paraconodont. Also associated are representatives of a new genus and species of intermediate morphology. The new species differs from *Prooneotodus rotundatus* in pos-

sessing a thin layer of apatite that covers a massive white basal cone. The white basal cone of this new species is virtually identical to the entire white element of associated *Prooneotodus rotundatus*, and a homology is strongly suggested between the basal cone of the former and the entire element of the latter. *Proconodontus tenuiserratus*, n. sp., differs from the new species only in possessing a small, faintly serrate posterior keel. The evolutionary relationships among these three kinds of elements may be clarified by histological investigations now in progress.

Proconodontus tenuiserratus is the ancestor of *P. posterocostatus*, which differs in having a more developed and nonserrate posterior keel. Two paratypes of *Coelocerodontus burkei* Druce and Jones (1971, text-fig. 22e, pl. 11, figs. 5, 6) are reassigned to this species. Elements in my collections from the Black Mountain section of Druce and Jones (1971) are identical to those from Texas.

Occurrence.—In the United States *P. tenuiserratus* is known from Texas (149 elements from upper Point Peak and lower San Saba members of Wilberns Formation, Llano uplift) and Oklahoma (three elements from the Fort Sill Limestone, Wichita Mountains). These elements are from the upper *Ellipsocephaloides* Zone in Texas and from the coeval upper *Saratogia* Zone in Oklahoma, both of late Franconian age. The species is also known from Australia (Druce & Jones, 1971).

Genus SEMIACONTIODUS Miller, 1969

Type species.—*Acontiodus (Semiacontiodus) nogamii* Miller, 1969, p. 421; by original designation.

Emended diagnosis.—Apparatus a symmetry transition of two types of erect to reclined simple cones; symmetrical elements more diagnostic but much less abundant than asymmetrical elements; anterior sides of both elements lacking costae or keels. Symmetrical element slightly compressed anteroposteriorly; lateral or posterolateral costae on both sides; posterior costa may be present; fine striae covering well-preserved elements. Asymmetrical element round to oval at base, base may be slightly expanded posteriorly; costa on one side, resulting in dextral and sinistral forms; broad groove often present posterior to costa. Basal cavity moderately deep; white basal cone often prominent. Most of cusp composed of white matter.

Discussion.—*Semiacontiodus* Miller was originally described as a subgenus of *Acontiodus* Pander. It was raised to genus rank by Lindström (1973, p. 437), and is recognized as such here. Lindström (1973) assigned several species described by Miller (1969) to this genus, including two described under different generic names. Because of different apparatuses, these latter species are reassigned here as *Monocostodus sevierensis* (Miller) and *Utahconus utahensis* (Miller).

Semiacontiodus is probably the ancestor of *Acontiodus* Pander, judging from similarity of the symmetrical elements; however, the apparatus of *Acontiodus* is unknown. *Acontiodus* elements have shallower basal cavities than do *Semiacontiodus* elements, and in *Acontiodus*, white matter is confined to a growth axis instead of comprising nearly the entire cusp as in *Semiacontiodus*.

Semiacontiodus bicostatus Miller, 1969, was described from broken elements. Subsequent collecting has not produced complete elements that can be surely assigned to this species. It is regarded here as an unrecognizable species and is not further considered.

SEMIACONTIODUS NOGAMII Miller

Figure 4V, W; Plate 2, figures 10-12

Acontiodus (Semiacontiodus) nogamii Miller, 1969, p. 421, text-fig. 3G, pl. 63, figs. 41-50; 1971, text-fig. 17A, pl. 1, figs. 1-4.

Semiacontiodus nogamii Lindström, 1973, p. 441-443.

Acodus housensis Miller, 1969, p. 418, text-fig. 3A, pl. 63, figs. 11-20; Jones, 1971, p. 43, pl. 3, fig. 6.

Oneotodus datsonensis Druce and Jones (part), 1971, p. 80, pl. 14, fig. 4 (*not* figs. 1-3).

Oneotodus erectus Druce and Jones, 1971, p. 80, text-fig. 26d, pl. 15, figs. 2-9; Jones, 1971, p. 57, pl. 3, fig. 8, pl. 8, fig. 8.

Oneotodus variabilis Abaimova and Markov, 1977, p. 93, pl. 14, fig. 11, pl. 15, fig. 4.

Emended diagnosis.—Symmetrical element with lateral costae only; posterior costa absent.

Discussion.—As listed in the synonymy, symmetrical elements of this apparatus were previously assigned to the form-species *Acontiodus (Semiacontiodus) nogamii*, *Semiacontiodus nogamii*, and *Oneotodus erectus*; the other form-species are asymmetrical elements. Similar stratigraphic ranges (Miller, 1978, table 2; Druce & Jones, 1971, text-fig. 18) and similar morphology indicate that these two element types represent a single apparatus.

Nogami (1967, text-fig. 3C, pl. 1, fig. 13) illustrated an element that was strongly compressed, and I earlier (Miller, 1969, p. 421) assigned it to *Acontiodus (Semiacontiodus) nogamii*. Because the element appears to be broken and its actual shape is uncertain, I here reject this earlier assignment.

I have studied the single element that Derby, Lane, and Norford (1972, text-fig. 3) assigned to *Acontiodus lavadamensis*. It lacks a posterior costa and is therefore a symmetrical element of *Semiacontiodus nogamii*.

The ancestor of *S. nogamii* is *Teridontus nakamurai* (Nogami). The elements of both species have a general similarity and both are ornamented with fine striae; however, *S. nogami* differs by having costae and lacking a circular cross section.

Semiacontiodus nogamii gave rise to *S. lavadamensis* by addition of a posterior costa to the symmetrical element. Asymmetrical elements of the two species are indistinguishable.

Occurrence.—*S. nogamii* is known in North America from Utah (upper Notch Peak and House limestones, House Range; Miller, 1969, 1978), Wisconsin-Minnesota (Miller, 1971), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), Pennsylvania-Maryland (upper Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), and from Alberta, Canada (Survey Peak Formation; Derby, Lane, & Norford, 1972). The species is associated with trilobites of the upper *Missisquoia typicalis* Subzone of the *Missisquoia* Zone and of the *Symphysurina brevispicata* Subzone of the *Symphysurina* Zone. It also is found in the *Clavohamulus elongatus* through *Clavohamulus hintzei* subzones of the *Cordylodus proavus* Zone (Miller, 1978). The species is known elsewhere from Australia (Druce & Jones, 1971) and the Soviet Union (Abaimova & Markov, 1977).

SEMIACONTIODUS LAVADAMENSIS (Miller)

Plate 2, figure 4

Acontiodus (Acontiodus) lavadamensis Miller, 1969, p. 420, text-fig. 3C, pl. 64, figs. 55-61.

Emended diagnosis.—Symmetrical element with lateral or posterolateral costae and also a central posterior costa, usually present only on distal part of element; asymmetrical element not distinctive.

Discussion.—This species was originally assigned to *Acontiodus (Acontiodus)* Pander. Because it apparently evolved from *S. nogamii* and probably shares with it an identical asymmetrical element, and because its cusp is composed almost entirely of white matter, it is reassigned to *Semiacontiodus* Miller.

Occurrence.—*S. lavadamensis* is an uncommon species known only from Utah (lower House Limestone, House Range; Miller, 1969, 1978), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), and Pennsylvania-Maryland (upper Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972). It is found in the *Hirsutodontus simplex* and *Clavohamulus hintzei* subzones of the *Cordylodus proavus* Zone and in the lower part of Fauna B of Ethington and Clark (1971).

Genus TERIDONTUS, new

Type species.—*Oneotodus nakamurai* Nogami, 1967, p. 216.

Description.—One-element apparatus consisting of symmetrical simple cones, usually erect to reclined; keels and costae lacking, microstriae may cover base and cusp; cross section circular to slightly oval; basal cavity moderately deep to shallow; cusp composed almost entirely of white matter.

Discussion.—Ethington and Brand (in press) have restudied type specimens of *Distacodus? simplex* Furnish, 1938, the type species of *Oneotodus* Lindström, 1955, and have concluded that they possess characters not present on elements of other species assigned to the genus. These characters include longitudinal ridges on the cusp, a recess on the posterior face in the region where the cusp is curved, and white matter completely enclosing the basal cavity. They describe one new species of *Oneotodus* consistent with the morphology of the type species and suggest that most other species of *Oneotodus* need to be reconsidered and reassigned to other genera. Following are my conclusions regarding the generic assignment of some of these species: *Oneotodus altus* Viira, 1970, ?= *Eoconodontus notchpeakensis* (Miller); *Oneotodus bicuspatus* Druce and Jones, 1971, questionably needs assignment to a new genus; *O. bulbousus* Miller, 1969, = *Clavohamulus bulbousus* (Miller); *O. datsonensis* Druce and Jones, 1971, = *Teridontus nakamurai* (Nogami); *O. erectus* Druce and Jones, 1971, = *Semiacontiodus nogamii* Miller; *O. gallatini* Müller, 1959, = *Prooneotodus gallatini* (Müller); *O. montanus* Lochman, 1964, is an unrecognizable species; *O. nakamurai* Nogami, 1967, = *Teridontus nakamurai* (Nogami); *O. tenuis* Müller, 1959, probably represents a new genus of protoconodont.

TERIDONTUS NAKAMURAI (Nogami)

Figure 4O; Plate 2, figures 15, 16

Oneotodus sp. a Müller, 1959, p. 458, pl. 13, fig. 17.

Oneotodus nakamurai Nogami (part), 1967, p. 216, text-figs. 3A, B, ?C (*not* text-figs. 3D, E), pl. 1, figs. 9, 12, ?13 (*not* figs. 10, 11); Miller, 1969, p. 435, text-fig. 5E, pl. 63, figs. 1-10; Druce and Jones (part), 1971, p. 82, text-fig. 26i (*not* text-fig. 26j), pl. 10, figs. 3, 4, 7, 8 (*not* figs. 1, 2, 5, 6); Jones (part), 1971, p. 58, pl. 4, figs. 1, 3, (*not* figs. 2, 4); Müller, 1973, p. 41, pl. 5, fig. 4; *not* Lee, 1975, p. 81, text-figs. 2E, G, pl. 1, figs. 6, 9, 10; *not* Abaimova and Markov, 1977, p. 92, pl. 14, figs. 12-14, 16.

Oneotodus datsonensis Druce and Jones (part), 1971, p. 80, text-fig. 26c, pl. 14, figs. 1-3 (*not* fig. 4); Jones, 1971, p. 56, pl. 3, figs. 5, 7.

Description.—Morphology simple but variable. Base long to short, narrow at basal margin, or may expand posteriorly; cusp erect to reclined, composed almost entirely of white matter that ends in sharp boundary transverse to cusp at point slightly above apex of basal cavity, tip of cusp may lack white matter; cross section circular or nearly so, with apex of basal cavity near center; surface of base and cusp covered by microstriae.

Discussion.—Nogami (1967, text-figs. 3D, E, pl. 1, figs. 10, 11) assigned to this species two paratypes that have the distinctive morphology of rounded elements of *Eoconodontus notchpeakensis* (see discussion under that species). These and similar elements assigned to *O. nakamurai* by Druce and Jones (1971, pl. 10, figs. 1, 2, 5, 6), Jones (1971, pl. 4, figs. 2, 4), Lee (1975, pl. 1, figs. 6, 9, 10), and Abaimova and Markov (1977, pl. 14, figs. 12-14, 16) are reassigned to *Eoconodontus notchpeakensis*. Some of the elements assigned to *O. nakamurai* by Jones (1971, pl. 4, figs. 1, 3) may represent *Eoconodontus notchpeakensis*, although they appear to be broken elements of a species of *Cordylodus*.

Druce and Jones (1971) described *Oneotodus datsonensis* and assigned to it elements similar to those of "*O.*" *nakamurai* but having more expanded bases and recurved cusps. I consider the shape of the base to be a variable feature in *Teridontus nakamurai*, and its holotype (Nogami, 1967, pl. 1, fig. 9) has a slightly recurved cusp. Therefore, the diagnostic features of *Oneotodus datsonensis* do not seem to be adequate to distinguish it as a separate species, and I consider it to be a junior subjective synonym of *T. nakamurai*. Because of a lateral costa, one paratype element of *O. datsonensis* (Druce & Jones, 1971, pl. 14, fig. 4) is reassigned to *Semiacontiodus nogamii* Miller.

Occurrence.—This is a cosmopolitan species. It is known in North America from Utah (upper Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (Whipple Cave Formation, southern Egan Range; Hales Limestone, Hot Creek Range), South Dakota (upper Deadwood For-

mation, Black Hills), Oklahoma (Signal Mountain Limestone in Arbuckle Mountains, reported by Müller, 1959, and Wichita Mountains), Texas (San Saba Member of Wilberns Formation and lower Threadgill Member of Tanyard Formation, Llano uplift), Pennsylvania-Maryland (Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), New York (Taconic allochthon; Landing, 1976a), and Vermont (Gorge Formation; Landing, 1978). Except for rare occurrences in the uppermost Franconian and lower Trempealeauan in Texas, *T. nakamurai* has not been found below the base of the *Cordylodus proavus* Zone in the United States. It occurs throughout the *C. proavus* Zone and is found in Fauna B of Ethington and Clark (1971). Outside of the United States, *T. nakamurai* is known from Alberta, Canada (Survey Peak Formation; Derby, Lane, & Norford, 1972), western North Greenland (Kurtz, 1977), East Greenland (Miller & Kurtz, 1979), Iran (Müller, 1973), Soviet Union (Abaimova & Markov, 1977), Korea (Lee, 1975), China (Nogami, 1967), and Australia (Druce & Jones, 1971; Jones, 1971). Although most of these occurrences are in strata of latest Cambrian and Early Ordovician age, several are older. The species in Australia is in strata equivalent to the Franconian Stage (middle Upper Cambrian) in North America, but it also occurs in Ordovician strata (Druce & Jones, 1971). Occurrences in Korea and China may also be older than the *Cordylodus proavus* Zone, although this is uncertain.

Genus UTAHCONUS, new

Type species.—*Paltodus utahensis* Miller, 1969, p. 436.

Description.—Apparatus consisting of two types of simple-cone elements that form a symmetry transition; elements proclined, compressed, usually bent laterally; basal cavity a round cone, diameter about equal to height; base a prominent cone modified by one or two large costae extending from basal margin to tip of cusp; cusp large and composed of white matter. Unicostate element usually asymmetrical with right or left lateral costa; rare symmetrical variants with posterior costa. Bicostate element usually asymmetrical with lateral and posterolateral costae; rare symmetrical variants with costa on each side. Unicostate element usually more abundant.

Discussion.—Elements constituting the apparatus of the type species of *Utahconus* were previously described as form-species of *Paltodus*, *Acodus*, and *Acontiodus* (Miller, 1969). Lindström (1973) referred these species to *Semiacontiodus*. Such procedure is not followed here because these species form an apparatus different from that of *Semiacontiodus*. Unicostate elements of *Semiacontiodus* have essentially round cross sections with a lateral groove, whereas unicostate elements of *Utahconus* have nearly triangular cross sections due to the large costa. Bicostate elements of *Semiacontiodus* are symmetrical and oval at the base, whereas bicostate elements of *Utahconus* are asymmetrical due to lateral bending and twisting of the cusp, and they are usually round at the base.

Utahconus differs from *Monocostodus*, n. gen., in having bicostate elements as well as unicostate elements.

UTAHCONUS UTAHENSIS (Miller)

Figure 3B, C, F, G; Plate 2, figures 1, 2

Paltodus utahensis Miller, 1969, p. 436, text-fig. 5F, pl. 63, figs. 33-40.

Acontiodus (Semiacontiodus) unicostatus Miller (part), 1969, p. 421, text-fig. 5F, pl. 64, figs. 46-48 (*not* figs. 49-54).

Acodus sevierensis Miller (part), 1969, p. 418, text-fig. 3H, pl. 63, figs. 21-24 (*not* figs. 25-32).

Scandodus furnishi Druce and Jones, 1971, p. 88, text-fig. 29, pl. 13, figs. 6-8, ?9.

Acodus tetrahedron Özgül & Gedik, 1973, p. 46, pl. 1, fig. 5.

Semiacontiodus utahensis Lindström, 1973, p. 442, 443, 449.

Semiacontiodus unicostatus Lindström, 1973, p. 442, 443, 447.

Emended diagnosis.—Bicostate element lacking posterior process; posterolateral costa extends to base in a smooth curve.

Discussion.—The bicostate element of this apparatus is the form-species *Paltodus utahensis* Miller, 1969. Unicostate elements were assigned to the form-species *Acontiodus*

(Semiacontiodus) unicostatus Miller, 1969, and *Acodus sevierensis* Miller, 1969. Holotypes of these species are here judged to be parts of different apparatuses. The holotype of *Acodus sevierensis* forms the basis for the type species of *Monocostodus*, n. gen., and several paratypes of *Acontiodus unicostatus* (Miller, 1969, pl. 64, figs. 49-54) are reassigned to *Monocostodus sevierensis* (see discussion under *M. sevierensis* for differences in morphology). The holotype of *Acontiodus unicostatus* is judged to be a part of the apparatus of *Paltodus utahensis*, and the former species is considered to be a junior subjective synonym of the latter. This two-element apparatus is here removed from *Paltodus* and made the type species of the new genus *Utahconus*. Several paratypes of *Acodus sevierensis* Miller (1969, pl. 63, figs. 21-24) are judged to be a part of the apparatus of *U. utahensis*, and they are reassigned to that species.

Druce and Jones (1971) reported elements of *Scandodus furnishi* from Australia. Lindström (1971, p. 39) stated that this species is hyaline. Most elements assigned to *S. furnishi* and illustrated by Druce and Jones (1971, pl. 13, figs. 6-8) have cusps that, rather than being hyaline, are composed entirely of white matter. These elements are judged to be bicostate elements of *Utahconus utahensis*. One of Druce and Jones' figured elements (1971, pl. 13, fig. 9) is from younger strata, and it more closely resembles *Scandodus furnishi*. Thus, *U. utahensis* may be the ancestor of *S. furnishi*.

A single element assigned to *Acodus tetrahedron* by Özgül and Gedik (1973, pl. 1, fig. 5) is reassigned to *U. utahensis* on the basis of its overall morphology and the species with which it is associated.

Utahconus utahensis apparently evolved from *Teridontus nakamurai*. It is apparently the ancestor of *U. tenuis*. The two species of *Utahconus* have indistinguishable unicostate elements and can only be identified from the bicostate elements if they occur together. *U. tenuis* differs from its ancestor in having an oistodiform bicostate element, i.e., the posterior process meets the posterolateral edge at a sharp, acute angle.

Occurrence.—*U. utahensis* is known in North America from Utah (top beds of Notch Peak and lower House limestones, House Range; Miller, 1969, 1978), Nevada (Hales Limestone, Hot Creek Range; upper Whipple Cave and lower House limestones, southern Egan Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), Texas (upper San Saba Member of Wilberns Formation, Llano uplift), Pennsylvania-Maryland (upper Stoufferstown Member of Stonehenge Formation; Tipnis & Goodwin, 1972), and Alberta, Canafa (Survey Peak Formation; Derby, Lane, & Norford, 1972). The species ranges from the base of the *Hirsutodontus simplex* Subzone through the upper *Cordylodus proavus* Zone (Miller, 1978, table 2) and into the lower part of Fauna B of Ethington and Clark (1971). Elsewhere the species is known from East Greenland (upper Dolomite Point Formation; Miller & Kurtz, 1979), Turkey (Özgül & Gedik, 1973), and Australia (Druce & Jones, 1971).

UTAHCONUS TENUIS, new species

Figure 4T; Plate 2, figures 5-7

Oistodus minutus Miller (part), 1969, p. 433, pl. 66, figs. 5-7 (*not* figs. 1-4); Özgül and Gedik, 1973, p. 48, pl. 1, fig. 21.

Holotype.—USNM 303432 (Figure 5T; pl. 2, fig. 7).

Description.—Bicostate element oistodiform and distinctive; small, asymmetrical, with round to oval basal margin; base a small cone about as high as wide, with a prominent basal cone; cusp of short to medium length, oval to strongly compressed laterally, with anterolateral and posterolateral sharp edges or costae extending from basal margin to tip; posterolateral costa meeting posterior extension of base at sharp acute angle; cusp bent laterally, twisted, and composed mostly of white matter. Unicostate element usually asymmetrical with right or left lateral costa.

Discussion.—The single element of this species originally figured as *Oistodus minutus* (Miller, 1969, pl. 66, figs. 5-7) and a similar element figured by Özgül and Gedik (1973, pl. 1, fig. 21) are here reassigned to this species. Study of additional material (at least 49 elements, mostly from Oklahoma) indicates that this is the bicostate element of a distinct

species assigned to *Utahconus*. This element evolved from the bicostate element of *U. utahensis* by strong posterolateral bending of the cusp. The unicostate elements of the two species are indistinguishable.

The bicostate element of this species is similar in overall morphology to that of slightly younger hyaline species of *Oistodus*. *U. tenuis* is not hyaline, and a relationship is possible between this species and other non-hyaline form-species that have been assigned previously to *Oistodus*.

Occurrence.—U. tenuis is known in the United States from Utah (lower House Limestone, House Range; Miller, 1969; identified as *Oistodus* n. sp. in Miller, 1978, table 2), Nevada (Hales Limestone, Hot Creek Range), Oklahoma (upper Signal Mountain Limestone, Wichita Mountains), and Texas (upper San Saba Member of Wilberns Formation, Llano uplift). It occurs from slightly above the base of the *Clavohamulus hintzei* Subzone of the *Cordylodus proavus* Zone to the lower part of Fauna B. *U. tenuis* is also known from East Greenland (top of Dolomite Point Formation; Miller & Kurtz, 1979) and from Turkey (Özgül & Gedik, 1973).

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EXPLANATION OF PLATES

All specimens are from either Threadgill Creek section (TC) of Barnes and Bell (1977), Wilberns Formation, central Texas; or Chandler Creek section (CC) of Stitt (1977), Fort Sill and Signal Mountain limestones, Wichita Mountains, Oklahoma. Sample designations include section prefix followed by height above base of Cambrian strata in meters (and feet): for example, TC 446 (1,460).

PLATE 1

Conodonts of *Proconodontus* Lineage

All X60, except 1-3 and 12, which are X120.

FIGURE

1-3. *Proconodontus tenuiserratus* Miller, n. sp.——*1.* Lateral view of partly exfoliated paratype with prominent basal cone and faint, only slightly serrated posterior keel, from TC 360 (1,180), USNM 303278.——*2.* Lateral view of holotype showing typical development of serrated posterior keel, from TC 357 (1,170), USNM 303277.——*3.* Lateral view of paratype with slightly serrated posterior keel, from TC 358 (1,165), USNM 303425.

4-6. *Proconodontus posterocostatus* Miller, n. sp.——*4.* Lateral view of holotype showing typical development of posterior keel, from TC 387 (1,268), USNM 303275.——*5.* Lateral view of robust paratype with tip broken, exposing prominent basal cone, from TC 387 (1,268), USNM 303276.——*6.* Lateral view of paratype with posterior keel extending from tip to base; partly exfoliated on anterior edge, exposing basal cone, from CC 342 (1,121), USNM 303423.

7. *Proconodontus muelleri* Miller. Element with anterior and posterior keels, from TC 409 (1,342), USNM 303422.

8. *Cambrooistodus minutus* (Miller). Compressed element from TC 419 (1,374), USNM 303281.

9. *Cambrooistodus cambricus* (Miller). Compressed element from TC 415 (1,360), USNM 303420.

10-12. *Eoconodontus notchpeakensis* (Miller). ——*10,12.* Symmetrical rounded element with smooth lateral face *(12)* lacking striae typical of *Teridontus* lineage, from TC 415 (1,360), USNM 303416.——*11.* Asymmetrical compressed element showing similarity to *Cambrooistodus* elements, from TC 415 (1,360), USNM 303417.

13. *Proconodontus serratus* Miller. Element with anterior and serrate posterior keels; tip broken, exposing tip of basal cone, from TC 415 (1,360), USNM 303424.

14,15. *Cordylodus proavus* Müller.——*14.* Rounded element with small round denticles well separated at bases, from CC 478 (1,557), USNM 303287.——*15.* Compressed element with prominent carina and sharp edges on cusp and denticles; bases of denticles more widely separated from each other than usual, from CC 530 (1,735), USNM 303288.

16. *Cordylodus intermedius* Furnish. Rounded element with round discrete denticles, from CC 565 (1,850), USNM 303285.

17. *Cordylodus intermedius?* Furnish or *C. drucei?*, n. sp. Compressed element with sharp-edged cusp and denticles (fused at bases), prominent carina; this type of element is associated with rounded element of *C. intermedius* and *C. drucei*, n. sp., from CC 567 (1,857), USNM 303286.

18,19. *Cordylodus lindstromi* Druce and Jones. ——*18.* Rounded element with round cusp and discrete denticles, from CC 569 (1,866), USNM 303414.——*19.* Compressed element with sharp edged cusp and denticles (fused at bases), lacking carina, from CC 569 (1,866), USNM 303415.

20,21,25. *Cordylodus drucei* Miller, n. sp.——*20,21.* Inner lateral view *(20)* and outer lateral view (21) of holotype, a rounded element with rounded cusp and discrete denticles, slightly rounded anterobasal corner, and prominent carina (20), from CC 545 (1,785), USNM 303283.——*25.* Inner lateral view of paratype, a rounded element with sharp anterobasal corner and prominent carina, from CC 545 (1,785), USNM 303284.

22. *Cordylodus angulatus* Pander. Rounded element with rounded cusp and discrete rounded denticles, from TC 447 (1,465, 5 ft above base of Tanyard Formation), USNM 304013.

23. *Cordylodus angulatus?* Pander or *C. rotundatus?* Pander. Compressed element with sharp edges of cusp and denticles (fused at bases), weak inner carina, from same sample as figure *22*, USNM 303283.

24. *Cordylodus rotundatus* Pander. Rounded element with strongly rounded anterobasal margin and prominent inner carina beneath first denticle, from same sample as *22*, USNM 303435.

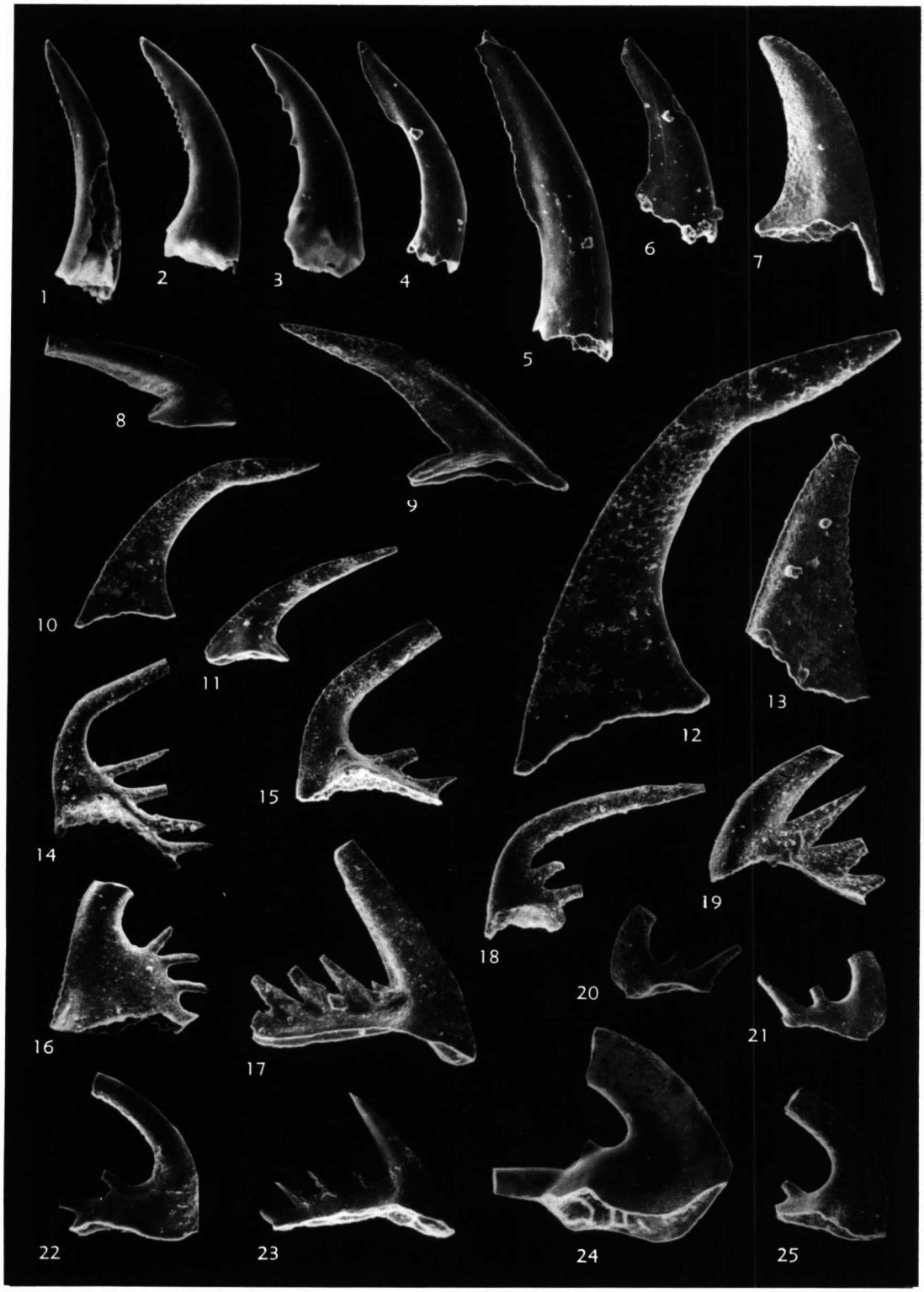
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PLATE 2

Conodonts of *Teridontus* Lineage

FIGURE

1,2. *Utahconus utahensis* (Miller).——*1.* Unicostate element with posterior sharp costa extending to base of cusp, USNM 303431.——2. Bicostate element with two lateral sharp costae extending to bottom of prominent round base (slightly broken on right basal corner), USNM 303430; *1,2* both from CC 530 (1,735), X60.

3. *Hirsutodontus rarus* Miller. Element with poorly developed cusp and nodose ornamentation (lacking on posterior face and around basal margin), from CC 455 (1,493), X120, USNM 303419.

4. *Semiacontiodus lavadamensis* (Miller). Element with oval base, two lateral costae flanked by prominent grooves, and central posterior costa near tip; faint vertical striae visible in posterior grooves, from TC 446 (1,460, about 19.2 m [63 ft] below top of Wilberns Formation), ×120, USNM 303428.

5-7. *Utahconus tenuis* Miller, n. sp.——*5.* Oblique anterior view of paratype, a bicostate element with anterior and posterior costae extending to base of oval cusp, which is bent to right side; broken tip shows cross section of cusp; USNM 303434.——*6.* Outer lateral view of paratype, a bicostate element with acute angle where posterior costa meets base, USNM 303433.——*7.* Inner lateral view of holotype, a bicostate element with acute angle near top of base, USNM 303432. All from CC 536 (1,756), all X60.

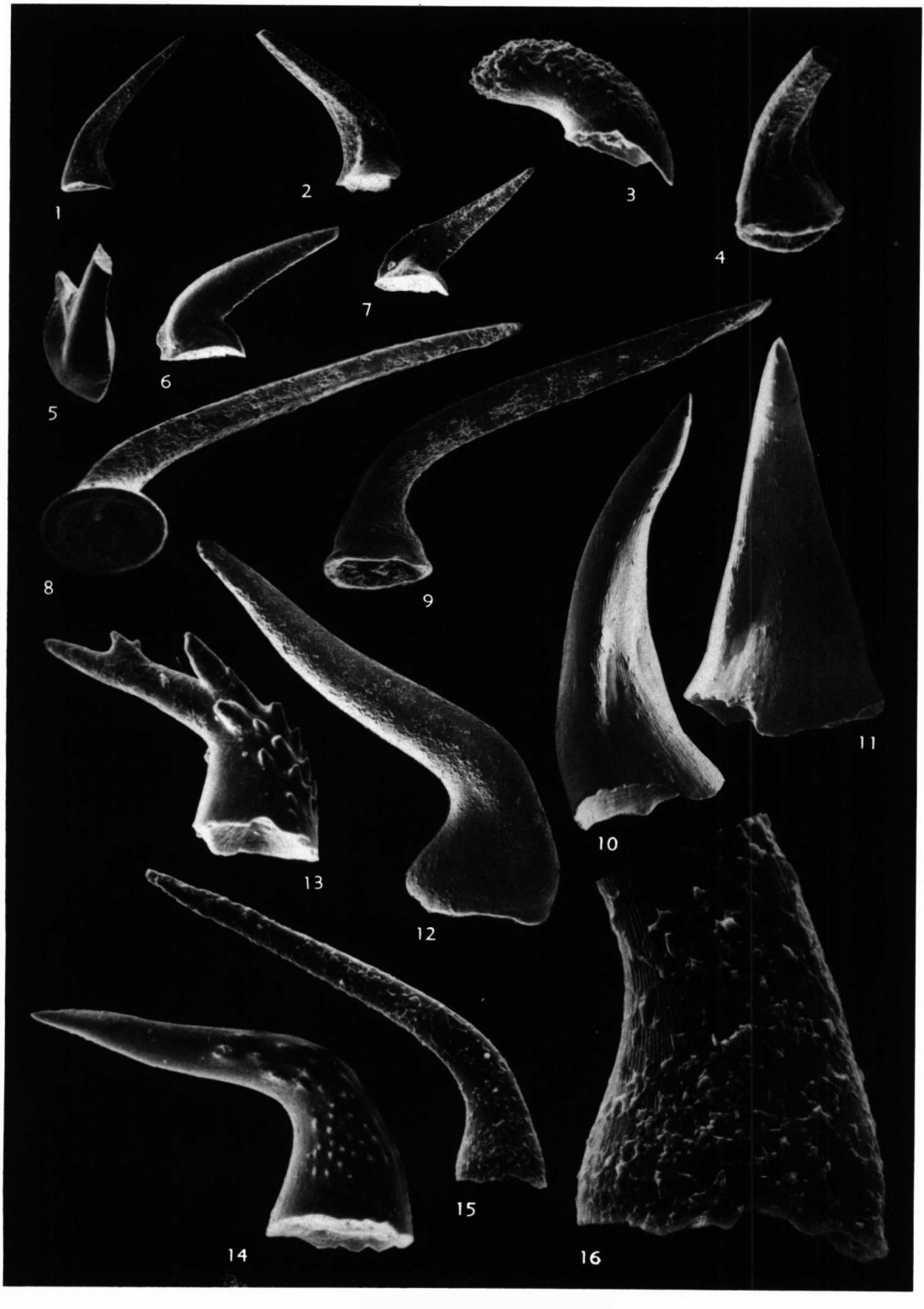
8,9. *Monocostodus sevierensis* (Miller).——*8.* Basal oblique view showing oval base and slender posterior costa that ends near bend of cusp.——*9.* Lateral view showing costa extending from near bend of cusp almost to tip; *8,9* from same sample as figure *4*, ×110, USNM 303421.

10-12. *Semiacontiodus nogamii* Miller.——*10,11.* Posterolateral (10) and posterior *(11)* views of prominently striated, symmetrical, bicostate element, showing lateral costae and adjacent grooves, lack of central posterior costa, and oval basal margin, from CC 567 (1,857), ×200, USNM 303426.——*12.* Lateral view of asymmetrical unicostate element with weak, broad lateral costa, from CC 465 (1,524), ×100, USNM 303427.

13. *Hirsutodontus simplex* (Druce & Jones). Lateral view of typically ornamented element with large spines; from same sample as figure *4*, ×120, USNM 303289.

14. *Hirsutodontus hirsutus* Miller. Lateral view of typically ornamented element with small nodes; from CC 465 (1,524), ×120, USNM 303418.

15,16. *Teridontus nakamurai* (Nogami).——*15.* Lateral view of slender element ×160.——*16.* Enlarged view of base of element in figure *15* showing fine striae typical of several species of the *Teridontus* lineage, but only visible on well-preserved specimens at high magnification; ×560, from TC section, 1.3 m (4 ft) below top of Wilberns Formation, USNM 303429.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